STUDIES ON GENETIC ARCHITECTURE AND PREDICTED RESPONSE IN BIOMETRICAL TRAITS OF SEXUALLY BREEDING *ARTEMIA*

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DECLARATION

I here by declare that this thesis entitled "Studies on genetic architecture and Predicted response in biometrical traits of sexually breeding *Artemia*" has not previously formed the basis for the award of any degree, diploma, associateship, fellowship or other similar titles or recognition.

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CERTIFICATE

Certified that the thesis entitled "Studies on genetic architecture and Predicted response in biometrical traits of sexually breeding *Artemia*" is a bonafide record of the work carried out by Mr. M. M. Shirdhankar under my guidance and supervision and that no part thereof has been presented for the award of any other degree, diploma or any other similar title.

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INTRODUCTION

INTRODUCTION

A major problem encountered by the aquaculturists is the availability of the right kind of food, especially the live food, for rearing the larvae and juveniles of the finfishes and shellfishes under controlled systems. *Artemia*, a phyllopodus small crustacean, popularly called as brine shrimp, have been used as an ideal food for finfishes and shellfishes throughout the world. They are being offered not only to the fishes, but also to other diversified groups of animals. It has been estimated that *Artemia* have been fed to more than 80 % of marine animals cultured so far, as a sole diet or in combination with other food sources (Kinne, 1977)

The life cycle of *Artemia* is composed of different stages like cyst, nauplii, metanauplii and adult, and interestingly all these stages are excellent live foods. The freshly hatched nauplii of *Artemia* are the most extensively used form. It has been estimated that over 2000 metric tons of *Artemia* cysts are hatched annually and the nauplii are used as live food (Stappen, 1996). The *Artemia* cyst, which is the dormant form of egg, is also an excellent and convenient source of food for larval rearing. The adult as well as pre-adult *Artemia* are also widely used as live food for shrimps, prawns and juvenile fishes. The role of *Artemia* as live food in crustacean hatcheries is very substantial.

Ingestibility of a food by the larval or the juvenile fish or shellfish is determined to a great extent by the size of the food particle in relation to the

mouth size of the predator (Vanhaecke & Sorgeloos, 1980a; 1983). The mouth size of larvae naturally restricts the size of food particles, which can be ingested. In general, the mouth size is correlated with body size, which in turn is influenced by egg size and period of endogenous feeding (i.e. yolk sac consumption period). As long as the nauplius size does not interfere with the ingestion mechanism of the predator, one may expect that the use of larger nauplii with high individual weight will be more beneficial (Vanhaecke & Sorgeloos, 1980a). The predator will indeed spend less energy in taking up a smaller number of larger nauplii to fulfil its food requirement (Vanhaecke and Sorgeloos, 1983). Thus, the nutritional effectiveness of food is considered to be dependent on its ingestibility, which in turn is dependent on its size and configuration. Vanhaecke & Sorgeloos (1980a) have observed wide variations among the different strains of Artemia with respect to the size of cysts, nauplii and adults.

The implications of the above findings are far reaching and calls for basic investigations aimed at determining the genetic aspects that are involved in the size variability of cysts, nauplii etc. of *Artemia*. It also calls for genetic manipulations for developing different lines/strains of *Artemia* of different size specifications to suit the requirements of various species of cultured animals. Selective breeding, as used in farm animals and plants, is the time-tested genetic manipulation technique which can play a major role in developing these lines However, before resorting to large-scale breeding programmes, it is essential to carry out selective breeding experiments and evaluate their response to selection.

Selective breeding in *Artemia* still remains a gray area with no reported work on these lines till date. Although, Leger *et al.* (1986) suggested that high heritability and wide variations in cyst could be exploited through selective breeding techniques, no such work have been carried out so far for the successful development of *Artemia*l strains producing mini cyst. Similar is the case with other traits also. Therefore, selective breeding experiment in *Artemia* is of paramount importance.

Formulation of any selective breeding programme calls for a proper understanding of the genetic architecture of the economically important traits of the population in hand. Though, *Artemia* has been described in the 18th century and extensively studied in the most diverse fundamental disciplines of biological sciences, there is an apparent lack of information on its quantitative genetic aspects. The genetic studies hitherto carried out are limited to the fields of biochemical genetics, molecular genetics, cytogenetics, evolution etc. There has been hardly any study reported so far, partitioning the phenotypic variability of the different traits into the variance components as well as to estimate the much needed parameters like the heritability, genetic correlation etc. These vital aspects are the prerequisites for the formulation of selection and breeding strategies. Although, Vanhaecke & Sorgeloos (1980a) reported the existence of wide variations in the naupliar size of various strains of *Artemia*, they did not go further to estimate genetic component of these size variations. Similarly, though, they observed a high degree of positive correlation between diameter of decapsulated cyst and naupliar length, as well as between volume of decapsulated cyst and naupliar volume, no information could be generated on the genetic

correlation. Thus, there seems to be a complete vacuum as far as the quantitative genetic knowledge of *Artemia* is concerned. This fact has prompted the present work entitled "Studies on genetic architecture and predicted response in biometrical traits of sexually breeding *Artemia*" with the aim of generating the much needed information on the heritability of the various biometrical and reproductive traits in *Artemia*. While the heritability estimates are needed for predicting the selection response, the genetic correlations between the various traits are essential for predicting the correlated response in them. In addition, the lifehistory characteristics such as age at first offspring, time between broods and percentage of encysted offsprings, female reproductive characteristics such as broods per female, offsprings per day per female, total offspring per female, pre-reproductive period, reproductive period and post-reproductive period of final selected populations are compared with the base population.

The objectives of the present study are as follows:

1. To characterize the *Artemia* with respect to its biometrical traits of importance.
2. To estimate the variability in the above traits and to partition the same into constituent components.
3. To estimate and compare heritability of various quantitative traits using different methods.
4. To carry out selective breeding in *Artemia* for naupliar size (length) and to estimate the genetic gain realized from selection.
5. To estimate correlated response in the unselected traits.


REVIEW
OF
LITERATURE

REVIEW OF LITERATURE

The first written record of the brine shrimp dates back to 1756 by Schlosser. Despite the primitive optical equipment available at that time, Schlosser's drawing are very clear and correctly show eleven pairs of thoracopods in the adult animal. Later, while giving its first scientific description, Linnaeus (1758) described the adult with only 10 thoracopods in it. The controversy continued until Audouin (1836) confirmed the observation made by Schlosser. Meanwhile its original name of *Cancer salinus*, as proposed by Linnaeus (1778), was changed to *Artemia salina* by Leach (1819).

The genus Artemia is a complex of several sibling and superspecies defined by the criterion of reproductive isolation. Endemic to Old World are *A. parthanogenetica* Barigozzi, 1974 (in Europe, Australia and Asia), *A. tunisiana* Bowen and Sterling, 1978 (the Mediterranean region), *A. urmiana*, Gunther, 1900 (from Iran) and *A. sinica* Yaneng, 1989 (from China). Endemic in the New World are *A. persimilis* Piccinelli and Prosdocini, 1968 (in Argentina) and *A. franciscana* superspecies (in Americas and the Caribbean). Within the superspecies are populations which are reproductively isolated in nature: *A. (franciscana) franciscana* Kellogg 1906, *A. (franciscana) monica* Verrill 1869 and *A. (franciscana) sp.* the cluster of populations in Nebraska, U. S.

Role of *Artemia* in aquaculture

One of the major differences between aquaculture and cattle rearing is that the larvae of the most aquatic animal species of commercial interest have to be

offered a live food, whereas the cattle accept inert diet throughout their life cycle (Kinne and Rosenthal, 1977). Culturing of zooplankton that normally constitutes natural food of fish and shrimp larvae, is either commercially unfeasible or technically hard to realise (Girrin and Person - Le Ruyet, 1977). As a result, the efforts of early pioneers to rear marine fish were hampered by inadequate and unsuitable larval food supplies (Shelbourne, 1968).

A very significant progress in aquaculture was the discovery by Seale (1933) in U.S.A. and Rollefsen (1939) in Norway, that 0.4 mm nauplius, larvae of *Artemia*, constitutes an excellent food source for newborn fish larvae.

Leger *et al.* (1986) stated that the ability of *Artemia* to form dormant eggs called "cysts" might be the reason why it has been designated as a convenient, suitable and excellent source of larval food. Furthermore, they have stated that after about 24 hours of incubation in seawater the cysts release free swimming nauplii that can be fed directly to the larvae of a variety of aquatic organisms as a live and nutritious source of food.

It is the combination of a number of desirable characters of nauplii *viz.* their biochemical composition, their very thin carapace and the fact they are swimming prey have made them an ideal food source. Kinne, (1977) reported that *Artemia* is a suitable food for most diversified group of organisms of the animal kingdom e.g. foraminifera, coelenterates, flatworms, polychaetes, squids, insects, chaetognathus and of course a wide variety of both marine and fresh water crustaceans and fishes. In his treatise on "Cultivation of marine organisms" he (Kinne, 1977) has indicated that "more than 85% animals cultivated thus far

have been offered with *Artemia salina* as food source, either together with other foods or more often as sole diet ".

It has been proved many times that a diet of live *Artemia* gives better results than any preparation made from dead brine shrimp (Serfling *et al.*, 1974; Carlberg and Van Olst., 1975; Beck, 1979). Flutcher (1980) suggested that the essential nutrients of *Artemia* are lost during freezing and freeze drying. It has been demonstrated that dried brine shrimp can be successfully used as protein source in pelletized diets for fish and shrimp (Deshman & Shigueno, 1972; Gabaudan *et al.*, 1980).

In most of the cases, brine shrimps are used as freshly hatched nauplii. Although outgrown larvae of *Artemia* are reported to be a better food than nauplii for many predators (Kelly *et al.*, 1977; Purdom & Preston, 1977), the fact that they have to be cultured for few days, has limited this type of application in many aquaculture hatcheries (Brouillet, 1977). Adult brine shrimps are harvested from saline biotops to be used as food for the larvae of lobster (Schesser and Gallagher, 1974) and the fresh water prawn *Macrobrachium rosenbergii* (Anonymous, 1978).

Several authors have indeed demonstrated the potential use of decapsulated cyst as a direct food source for decapod larvae (Lavena and Figueroa, 1978; Sorgeloos, 1979; Mock *et al* ., 1980; Royan, 1980; Sorgeloos *et al.*, 1983 ; Wickenfeld *et al.*, 1984) and fish larvae (Sorgeloos *et al.*, 1977; De los Santos *et al.*, 1980; Devrieze, 1984; Nanayakkara *et al.*, 1985). Most of the usage of decapsulated cyst seems to be in penaeid shrimp hatcheries, wherein the post larvae are more able to withstand extra aeration needed to keep decapsulated

cysts in the column, but also can capture particles at or near the bottom of the tank in better manner (Bengtson *et al.*, 1991).

The principal food during the first week of larval rearing in aquaculture production around the world is *Artemia* nauplii (Corbin *et al.*, 1983). It has been in use for the commercial cultivation of penaeid shrimp species (Heinen, 1976; Hanson & Goodwin, 1977; Liao *et al.*, 1993), since 1956 when Hudinaga for the first time successfully reared *Penaeus japonicus* using *Artemia* nauplii (Liao *et al.*, 1993),

The *Artemia* nauplii are also used as a convenient food for the larvae of various fishes like cyprinids (Meske, 1973; Strowband and Dabrowski, 1981), flat fishes (Shelbourne, 1968; Dye, 1980), bass (Girrin, Barahona-Fernandes and Le Roux, 1975; Barahona -Fernandes and Girrin, 1977), bream (Person - Le Ruyet and Verillaud, 1980), white fish (Gunkel, 1979; Fluchter, 1980), cat fish (Hogendoorn, 1980) and sturgeon (Gun'ko, 1962).

Prey catching, handling and ingestion ability of the predator species differ from species to species and mostly depend on the size of the prey *vis-a-vis* mouth size of the predator. Thus, the size of cyst, nauplii, metanauplii and adult *Artemia* dictates its usefulness as a live food.

Sick & Beaty (1975) showed that while *Macrobrachium rosenbergii* stage VIII could not ingest sufficient amounts of *Artemia* nauplii to give a positive energy balance, it yielded better results in growth, development and survival rate with 5.5 mm juvenile *Artemia* as food. Purdom and Preston (1977) came to the same conclusion for the turbot larvae also. Several other authors (Dugan *et al.*, 1975; Smith, 1976 & Person - Le Ruyet *et al.*, 1978) have applied the technique

of feeding the advanced stages of nauplii like metanauplii, juvenile etc. to fish and crustacean larvae.

Pre-adult or adult *Artemia* are known to be a much better reference diet than formulated feeds for many of the aquaculture organisms like *Homarus americanus* (Hugher *et al.*, 1974; Gallagher *et al.*,1976), *Macrobrachium rosenbergii* (Aquacop, 1977), *Penaeus kerathurus* (San Feliu *et al.*, 1976) *Penaeus aztecus* (Venkataramiah *et al.*, 1975), *Callinectus sapidus* (Milliken *et al.*, 1980), *Solea solea* and *Scophthalmus maximus* (Aronovich and Spektorova, 1971), *Sparus auratus* (Alessio, 1974), *Dicentrarchus labrax* (Barahona - Fernandes and Girrin, 1976). Another popular use of *Artemia* is as a food for tropical and ornamental pet fishes (Sorgeloos, 1979 and Lai *et al.*, 1987).

Biometrics traits of *Artemia*

Cyst diameter

Differences among geographical strains of *Artemia* with regards to size of cyst and nauplii have been extensively studied by Vanhaecke & Sorgeloos (1980a). They made the detailed study of seventeen geographical strains. While the size of the hydrated untreated cyst ranged from 222.9 µm to 282.9 µm, the size of hydrated decapsulated cyst ranged from 207.3 µm to 266.3 µm depending upon the geographical region of origin. Differences between capsulated (untreated) and decapsulated cysts were not consistent, and revealed a variation of 3 µm to 13.35 µm in chorion thickness (Vanhaecke, 1983). Cysts from the San Francisco Bay and North Eastern Brazil tend to be among the smallest available whereas, those from India, China, Italy and France are among the largest. Data for the above and other strains can be found in the work of D'Agostino (1965), Wickins

(1972), Claus *et al.* (1977), Ucal (1979), Amat (1980), Vos *et al.* (1984), Nanayakkara *et al.* (1985) and Van Ballaer *et al.* (1985).

D'Agostino (1965) reported that within the same strain, the mean egg size remained constant between different batches, which were collected during different periods of the year. Cyst size appears to be genetically determined, since no appreciable size differences were found between cyst of different harvests obtained from the same source (Vanhaecke & Sorgeloos, 1980a) and between cysts produced from the same inoculum but in different countries (Vos *et al.*, 1984). Vanhaecke & Sorgeloos (1980a) have further confirmed the findings of D'Agostino (1965) and Claus *et al.* (1977). However, in a few cases, Vanhaecke & Sorgeloos (1980a) reported significant differences among cyst batches of same strains i.e., laboratory produced versus original material and cyst collected from populations transplanted into different countries versus their parental stock (seeding) material.

Vanhaecke & Sorgeloos (1980a) stated that the consistency in cyst size of San Francisco Bay strain harvested from natural populations as well as from laboratory grown populations confirmed the earlier observations made by D'Agostino (1965) on the Great Salt Lake *Artemia*.

Vanhaecke *et al.* (1987) suggested that the cyst diameter is controlled both by genetic and environmental factors. Further, it was reported, based on the values obtained from the crossbreeds, that the cyst diameter is inherited more from mother and not equally inherited from both parental strains (Vanhaecke *et al.*, 1987). Instead of being intermediate between strains of both the parents, the cyst diameters of cross breeds is approximately closer to that of female parent

strain, irrespective of the male population crossed with. It was thus concluded that genetic factors determining cyst diameter are sex linked.

Naupliar Dimension

Naupliar size of different *Artemia* strains have been studied by D'Agostino (1965) , Claus *et al.* (1977) and Claus *et al.* (1979). They observed remarkable size difference between nauplii of different strains. However, most of the information available on naupliar length and volume is due to the result of the comparative studies by Vanhaecke & Sorgeloos (1980a) and Vanhaecke & Sorgeloos (1983).

Vanhaecke & Sorgeloos (1980a) studied the naupliar length, dry weight, organic weight and ash content of nauplii of seventeen strains collected from fourteen countries. They found that while large variations exist in dry weight of nauplii from different geographical strains, no significant difference is seen within the same strain. They reported that the size of freshly hatched instar-I nauplii ranged from 428 to 517 μm depending on the strain. From the data presented by them (Vanhaecke & Sorgeloos, 1980a) the maximum size difference between largest and smallest nauplii is less than 100 μm.

Vanhaecke & Sorgeloos (1983) have reported that significant differences exist in the body volume of *Artemia* nauplii of different strains with maximum difference occurring between those of San Francisco Bay strain and Italian parthanogenetic strain. The largest nauplii are produced by parthanogenetic strains with high degree of ploidy.

Growth and adult body size

Salinity and temperature of external medium exert tremendous influence in the growth and size of *Artemia*. The adult size of *Artemia* has an inverse relationship with salinity of external medium (Martin and Wilbur, 1921; Heath, 1924; Bond, 1933 and Warren, 1938). According to Weisz (1946), the growth rate of *Artemia*, from hatching to sexual maturity, is directly related to the salinity of external medium. Reeve (1963) reported maximum growth in *A. franciscana* (Utah strain) in 35 ppt salinity at 20°C. Baid (1963) compared the growth rates of *Artemia* females cultured in 125 ppt and 65 ppt salinities and found that the growth rate was higher in the former. Sick (1976) could obtain 6.0 mm size *Artemia* on 16^{th} day in 33 ppt salinity at 25°C. Royan (1980) recorded 10.2 mm *Artemia* on the 19^{th} day at 25°C.

Vanhaecke & Sorgeloos (1980b) did the comparative studies between the reference strain (San Francisco Bay strain, batch 288-2596) and other strains. They recorded the average length of 7 days old larvae as 3.16 ± 0.17 mm. Differences in growth rates among the various geographical strains were reported by them. Compared to the reference strain they recorded slower growths in brine shrimp from Larnaca Salt Lake, Santa Pola, Salin du Giraud and an unknown locality in China but higher growth rates in samples from Adelaide, Manure, Bahia Salinas, Great Salt Lake, Buenos Aires, Galera Zamba and Chaplin Lake.

Wear & Haslett (1986) recorded a mean length of 12 mm in *A. franciscana* from Lake Grassmere when grown at temperature and salinity ranges from 17 to 26°C and 140 to 200 ppt respectively. In the same study 11.0 mm and 14.0 mm mean lengths were recorded for male and female

respectively in 140 ppt at 17°C. In 260 ppt salinity, *Artemia* females and males did not grow beyond the total mean length 8.0 mm and 7.5 mm respectively at any experimental temperature.

Gajardo *et al.* (1992) have reported the maximum, minimum and mean lengths of *Artemia* from Chilean Andes as 9.0 mm, 7.10 mm and 8.04 mm respectively at 22 °C temperature and 60 ppt salinity.

Triantaphyllids *et al.* (1995) compared the growth of *Artemia* in different salinities. Parthanogenetic population *viz. A. parthanogenetica* from man made salterns near the city of Tanggu, Tianjin province and bisexual population *viz. A. franciscana* from San Francisco Bay (California, USA) were grown in different salterns. Minimum mean total length of 5.27 mm was recorded in 180 ppt salinity and maximum total length of 10.57 mm in 60 ppt salinity on 26 day old *Artemia* from Tanggu. Whereas, in San Francisco Bay strain minimum recorded mean length was 6.37 mm in 180 ppt salinity and maximum recorded mean length was 10.16 mm in 35 ppt.

Later, Triantaphyllids *et al.* (1997) performed morphological and allometrical studies with adult males and females of 11 bisexual populations of *Artemia.* In males, the minimum total length of 8.75 mm recorded was in San Francisco Bay, while maximum total length of 12.37 mm was in Urmiana Lake strains. In females also the trend was same with minimum length of 11.14 mm in San Francisco Bay and maximum length 16.35 mm in Urimiana strains. In, the Great Salt Lake strain (Argent-I grade), the recorded total length was 9.22 mm for males and 12.51 mm for females. In another Great Salt Lake sample (Argent pt. grade), these records were 8.41 mm and 10.83 mm

respectively. The statistical analysis of biometrical data showed that Great Salt Lake (Argent pt. grade) group of *A. franciscana* is morphologically closer to San Francisco Bay strain than the Great Salt Lake (Argent -I grade) strain.

Lifehistory and reproductive traits

According to Jensen (1918), the *Artemia* from Great Salt Lake, when reared in the laboratory at room temperature in brine of unspecified salinity, became sexually mature within 18 to 21 days after hatching.

Barigozzi (1939) measured the average time of development from hatching to sexual maturity in three populations of brine shrimp, *viz.* bisexual animals from America, parthanogenetic females from south of France and North Italy, cultured in the laboratory using 18-20 °C artificial sea water. The mean age at sexual maturity of the three populations varied between 22 to 28 days. However, these differences were not significant.

Weisz (1946) reported that animals reared in dilute brine of 30 ppt salinity became sexually mature in about 32 days after hatching, while those reared in more concentrated brine of 115 ppt salinity attained sexual maturity in about 22 days.

Von Hentig (1971) studied the influence of salinity and temperature on various life processes of *A. salina* from Great Salt Lake, Utah, USA and concluded that while the maturation rate, onset of reproduction, interval between clutches as well as total number of offspring are primarily influenced by temperature, the clutch size is a function of salinity. He further reported that at low temperatures, reproduction is possible only at high salinities.

Tobias *et al.* (1980) studied the sexual maturity in 17 geographical strains of *Artemia* and observed wide variations in them. While Santa Pola strain (China) matured on 21st day, Buenos Aires (Argentina) strain attained maturity on the 11th day itself. In the Great Salt Lake strain, maturity was attained on the 13th day.

Wear *et al.* (1986) studied maturation, fecundity and generation time in *A. franciscana*. They reported that the males and females mature at 7.0 mm size in 80 to 140 ppt salinity and a temperature of 14 to 32°C. In higher salinities of 200 to 260 ppt, maturity was achieved at 6.0 to 6.5 mm size. At 8°C temperature and 140 ppt salinity, maturity was achieved at a total length of 5.0 mm. They observed that the time for 50 % maturity was shortest (9 1/2 days) at 26°C temperature with 140 ppt salinity. The minimum generation time in 80 ppt salinity was two days at 26°C while maximum was 5 days at 14°C.

Wear *et al.* (1986) also studied the number of offsprings produced per batch. Salinity of 140 ppt and temperature of 26°C resulted in maximum number of progeny, the average being 125.1 nos. At 260 ppt and 26°C, the mean number of offspring was minimum *viz.* 29.4 nos.

Studies by Wear *et al.* (1986) showed that at 140 ppt, the time required for the next generation were 13 and 14 days at 32 and 26°C respectively. They also recorded that the generation time exceeded 50 days at a temperature lower than 14°C and at 32°C, or at salinity beyond 80 ppt.

Reproductive pattern and mode of reproduction in 60 ppt salinity were studied by Browne (1980, 1982) while fecundity has been studied in detailed by

Browne *et al.* (1984). They have recorded the lowest average number of broods (30.60) per female in the Indian strain (Madras) and maximum average broods (53.25) per female in the San Francisco strain, California (USA).

Heritability

Heritability is one of the important properties of quantitative traits. It expresses the proportion of total variance that is attributable to the average effect of the genes. The term 'heritability' is used both in narrow as well as in broad sense. In a narrow sense, it is defined as the ratio of the additive genetic variance to the total phenotypic variance (Lush, 1940). Heritability in the broad sense is the ratio of the total genetic variance to total phenotypic variance. The total genetic variance includes additive genetic as well as variance due to dominance deviation and epistatic interaction. The genetic interpretation of various components of variance have been presented by Lerner (1958). Falconer (1960) defined heritability as the regression of breeding value on phenotypic value ($h^2 = b_{GP}$), which is equivalent to the square of correlation between breeding values and phenotypic values ($h^2 = r^2_{GP}$).

The importance of heritability in a breeding experiment lies in its predictive role expressing the reliability of phenotypic value as a guide to the breeding value. It is of immense use in making decisions regarding the type of selection methods which will allow the greatest or most rapid improvement or both. Heritability, in narrow sense, is most reliable for predicting the genetic gains from selection. The genetic gain expected from selection is the function of heritability, selection intensity and standard deviation of the trait. For example, when a trait is highly heritable, the most economical and rapid improvement is

likely to be made through mass selection. On the other hand, when it is lowly heritable, one or other forms of family selection or progeny testing, or both, are likely to be more effective than mass selection. Thus, heritability estimates are necessary to a breeder for planning the breeding system and predicting response to selection, besides genetic evaluation of selection programme.

For any trait, an average of heritability estimates, obtained from many populations, is useful only to categorize the expected gains in another population as large, medium or small. If one is interested in predicting genetic gain in a specific population as accurately as possible, then he must first estimate the heritability from the population for which prediction is to be made.

Several methods are available for estimating heritability, such as sib correlation, regression of offspring on parent etc. (Lush, 1949; Lerner, 1950; Kempthrone, 1957 and Falconer, 1960).

Heritability from sib correlation

Perhaps the most popular method for estimating heritability in animal breeding is sib correlation. Both full sib as well as half sib correlations can be utilized for estimation of heritability.

Heritability based on sib correlation method is usually calculated from variance component analysis. Common statistical model, used for estimation of heritability from variance component analysis, is that of King & Handerson (1954).

Single pair mating is one of the several mating designs available for estimation of heritability from sib correlation. This can be followed in multiparous animals such as swines, rats or mice and birds like quails, chickens, turkeys etc. or any other species which produce large number of progenies in a

short time (Becker, 1975). Therefore, it is also useful in case of many aquatic species. In this design, the mating produces several offspring simultaneously which are full sibs. The various components obtained from the analysis of such data is equivalent to covariance of full sib.

The components of covariance of full sib are as under:

$\sigma^2_S = Cov_{FS} = 1/2\ V_A + 1/4\ V_D\ 1/4\ V_{AA} + 1/6\ V_{DD} + 2/16\ V_{AAA} + ...etc.$

$\sigma^2_W = \sigma^2_T - Cov_{FS} = \sigma^2_T - \sigma^2_S = 2/4\ V_A + 3/4 V_D + 3/4 V_{AA} + 14/16\ V_{AD} + 15/16\ V_{DD}$

$+ 14/16\ V_{AA} + ... etc.$

The sire component of variance (σ^2_S), thus estimates ½ of additive genetic variance, 1/4 of dominance variance and various amounts of epistatis variance. The σ^2_W component of variance estimates the reminder of the genetic effect plus the environmental variance.

The standard error, which provides information regarding the precision of the estimates, is uncomfortably high unless the number of individuals measured are fairly large (Falconer, 1981). The total number of such individuals that can be measured are limited by space, labour and cost. When number of individuals measured per family are increased, the number of families that can be measured are reduced. Hence, a compromise between large families and many families are essential. It also helps to minimise the sampling variance of the correlation or regression.

Falconer (1981) and Pirchner (1983) presented various formulae to calculate standard errors of heritabilities estimated from regression and sib

correlation methods. Hill & Nicholas (1974) developed formula for covariance relating to several important combinations in order to combine heritability estimate from offspring parent regression and sib analysis.

Heritability is influenced by environment to which the individuals are subjected. Several studies have shown that different environment changes the heritability. McLaren (1976) observed that age at sexual maturity in copepod *Eurytemora hardmani* is highly heritable (0.71) only in females, if grown at 15°C. When grown at 10°C, the magnitude of the heritability estimates decreased considerably and there was no detectable maternal effect. On the other hand, the results in male offspring were more or less consistent at both the temperatures.

Although heritability is essentially a property of trait, it is also a property of population, and varies from population to population. Its values for body size of larvae and postlarvae in *Penaeus vennamei* and *P. stylirostris* are highly fluctuating (Lester, 1988), with large errors that encompassing the whole range of heritability from 0.0% to 100.0 %.

Since the value of heritability depends upon the magnitude of different components of variance, a change in any one of them will definitely affect it. Heritability estimate for the same trait may vary with age. Lester & Lawson (1990) estimated the heritability of size at different ages. Heritability estimates for size ranged from 0.0 to 0.16 after larval growth and 0.0 to 0.59 after post-larval growth

Falconer (1960) suggested that heritability estimates derived from paternal half sib correlation are more reliable, since, they are least affected by environmental variations. On the other hand, estimates derived from maternal half

sib correlation are more biased since they are likely to be confounded with maternal effects and/or dominance deviations. The heritability estimates obtained from full sib correlation method is expected to be somewhat intermediate between paternal and maternal half sib correlation methods in values, so also with regards to degree of bias (Jerome *et al.*, 1956). Robertson (1959a) stated that the estimates based on full sib correlations are subjected to the large sampling variations and as such sample size should be substantially large to place any reliability of this method. The heritability estimates based on full sib correlation contain a portion due to dominance deviation, and in principle, such estimates should be larger than those obtained from parent offspring regression.

Although there is an abundance of heritability estimates reported for various traits of live stocks, and to a lesser extent of fishes, there are no reports of the heritability estimates from *Artemia*. Though, Browne *et al.* (1984) estimated the genetic component of number of traits in *Artemia*, there have been no attempts to estimate the heritability of any of the quantitative traits using the standard procedure. The genetic portions of the traits estimated by them are as under.

Offspring per brood (42.66 %), broods per female (23.06 %), offspring per day per female (58.79 %), period between broods (56.09 %), percent offspring encysted (0.0 %), percent cyst hatched (0. 0%), total offspring per female (41.74 %), female pre-reproductive period (55.71 %), female reproduction period (31.33 %), female post-reproductive period (0.0 %), total female life-span (3.67 %) and total male life-span (28.48 %) for all sexual populations. They (Browne *et al.*, 1984) have also estimated the maximum genetic component from

Old World sexual populations as 62.23% for period between broods and minimum as 19.72 % for total female life-span.

According to Tackaert *et al.* (1987), cyst diameter is a genetically controlled characters in *Artemia* which is not equally inherited from both paternal strains, but rather more from mother shrimp. They also observed that temperature resistance is also under genetic control.

The heritability estimates reported for some of the other aquatic animals are presented here under :

Gall (1975) observed a reduction in heritability of growth with age in the rainbow trout. While the heritability of early growth was around 50%, and the weight at one year of age had a low heritability of 20 %.

McLaren (1976) studied the heritability of adult size in copepod, *Eurytemora herdmany*, and indicated that it was highly heritable (0.97) only in males, when grown at 15°C. But, at 10°C, the estimates of heritability were quite low and non-significant. He also observed strong maternal effects.

Klupp (1979) has estimated heritability in rainbow trout at 1.06 ± 0.49 for weight on 125 days of age and 1.05 ± 0.60 for head length on 68 days age. While heritability estimate for head length on 184 days of age was 0.65 ± 0.32, heritability of all other traits were higher than this value.

In rainbow trout, the heritability for number of eggs per brood, estimated from full sibs data, were 0.19 ± 0.06 (Gall, 1975), 0.44 (Gall & Gross, 1978) and 0.50 ± 0.17 (Haus, 1984), but was 0.33 ± 0.20 when estimated from sire data (Haus, 1984).

The estimated heritability of weight and length in Atlantic salmon were 0.08 and 0.12 respectively from sire component of variance, but were 0.15 and 0.17 respectively from dam component (Refstie and Steine, 1978).

Refstie (1980) estimated a low heritability value of 0.06 for three years class body weight in the rainbow trout from the sire component of variance. However, the values derived from dam component of variance were 1.32 and 1.04 from unadjusted and adjusted data (for environmental effects) respectively.

Heritability of slaughter weight of rainbow trout reared in seawater for 18 months was estimated from full sib data by Gunnes & Gjedrem (1981). The estimates from sire and dam components were 0.55 and 0.03 respectively. Pooled heritabilty estimates from the sire components were as 0.17 and 0.23 for weight and length respectively.

Busak (1983) estimated heritability for 56 day's weight by half sib and full sib analysis in mosquito fish *Gambusia affinis* as 0.16 and 0.21 for male 0.60 and 0.86 for female respectively.

Busak & Gall (1983) estimated heritability for 60 days weight as 0.25 for male and 0.77 for females in mosquito fish *Gambusia affinis*.

Bondari *et al.* (1983) obtained a moderate heritability of 0.38 for females and 0.20 for males in high body weight line, indicating a sufficient level of additive genetic variance for the improvement of growth rate in the channel catfish.

In Atlantic salmon, heritabilities estimated by Halseth (1984) were 0.37 ± 0.16 and 0.30 ± 0.16 from full sib and half sib family data respectively.

In mussel *Mytilus edulis*, Mallet *et al.* (1986) reported the heritability of larval shell length from the dam component ($h^2 = 0.19 \pm 0.04$) to be approximately as large as the heritability based on the sire component. In the same report, the heritability for shell length of adults maintained at two environments, *viz.* Env-1 and Env-2 were 0.92 ± 0.27 and 0.22 ± 0.07 respectively. Further, they reported the heritability for juvenile shell length as 0.62 ± 0.06.

After 10-years of selection and breeding in coho salmon, the heritability estimated for 8th month body weight, through full sib analysis, by Hershberger *et al.* (1990) ranged from 0.48 to 0.66.

Guo-Sheng Su *et al.* (1996) estimated low heritability values ranging from 0.03 to 0.13 for body weight in rainbow trout *Oncorhynchus mykiss*. They also reported that heritability estimate tends to increase with age; being lowest (0.05) at 168 days but highest (0.10) at 336 and 364 days.

Taniguchi *et al.* (1996) reported in gynogenic diploid ayu (*Plecoglossus attivelis*), a heritability of 0.795 for fork length, 0.811 for standard length and 0.681 for body weight at 9 months of age. The heritabilities were relatively high (> 0.5) for 5 morphometric traits *viz.*, head length, snout length, upper jaw length, orbit diameter and depth of caudal peduncle and 3 metric traits dorsal fin rays, pelvic fin rays and vertebrae. The heritabilities were rather intermediate ($0.2 < h^2 < 0.5$) for 5 traits *viz.* lower jaw length, body depth, body width, preanal length and caudal peduncle length but low for 3 trait *viz.* trunk length, pectoral fin rays and anal fin rays.

Heritability estimates based on variance component analysis may be subjected to large sampling error and may be over estimated because of sex linkage and maternal as well as non-additive genetic effects.

Heritability, estimated for total length as well as wet weights at 6 and 10 weeks of age in *Penaeus monodon* were approximately 0.10 (Benzie *et al.*, 1997). The dam components of both total length and weight were reduced from 0.5 to 0.6 at 6 weeks to 0.3 to 0.4 at 10 weeks of age. The reduction in dam component with age is suggestive of large non-additive genetic and/or common environmental effects.

Although theoretical limits of heritability estimates are 0 and 1, there are number of reports of heritability estimates which are out side these values, pertaining to a number of domestic animals and fishes. Some of these reports pertaining to the aquatic animals are presented in Table – 1. There are no reports of heritability estimated from sib data in *Artemia*.

Heritability estimates from regression of offspring on parent

The resemblance between the relatives is the basic genetic phenomenon displayed by metric characters. The degree of resemblance is the property of character that can be determined by relatively simple measurements made on the population without any special experimental techniques. The degree of resemblance provides the means for estimating the amount of additive genetic variance. An understanding of the causes of resemblance between the relatives is, therefore, fundamental to the practical study of metric characters and its application in the animal and plant improvement programmes.

Table 1 Heritability estimates outside the theoretical limits *reported in literature*

Species	Traits	Heritability	Methods of estimates	Author
Rainbow trout	630 days of weight *in kg*	1.04 ±0.12	Family component of variance	Gall and Gross (1978)
Rainbow trout	125 days weight	1.06 ±0.49	Family component of variance	Klupp (1979)
Rainbow trout	140 days weight	1.04	Dam component of variance	Refstie (1980)
Rainbow trout	Dead fry	-0.02 ± 0.01	Sire component of variance	Kanis *et al.* (1976)
Rainbow trout	2 year Weight	-0.01 to 0.34	Sire component of variance	Gunnes and Gjedrem (1981)
Rainbow trout	2 year length	-0.03 to 0.32	Sire component of variance	Gunnes and Gjedrem (1981)
Rainbow trout	K - factor	-0.02 to 0.06	Sire component of variance	Gunnes and Gjedrem (1981)
Tilapia	90 days length	-0.02 ± 0.07	Dam component of variance	Tave and Smitherman (1980)
Fresh water prawn	311 days weight male (g)	-0.14 ± 0.25	Sire component of variance	Malecha *et al.* (1984)
Erytemora herdmany	Age at maturity	1.13	Dam within sirecomponent of variance	McLaren (1976)
Channel catfish	30- days length	1.22 ± 1.11	Sire component of variance	Regen (1979)
Channel catfish	150 days length	1.13 ± 0.92	Sire component of variance	Regen (1979)
Channel catfish	Fry mortality at 1.1 ppm dissolved oxygen	0.9 ± 0.3 to 1.7 ± 0.1	Sire component of variance V_D	Durborow *et al.* (1985)
Brown trout	% Dead eyed egg	-0.01± 0.01	Sire component of variance	Kanis *et al.* (1976)
Brown trout	Number of pyloric caeca	1.10 ± 0.26 to 0.10 ± 0.0	h^2S	Bergot *et al.* (1976)
Brook trout	Survival to 144 days	-0.04 ± 0.04	Sire component of variance	Robison & Luempert (1984)
Brook trout	Survival to 243 days	- 0.02 ± 0.04 to 0.10± 0.0	Sire component of variance	Robison & Luempert (1984)
Atlantic salmon	K factor, 3-year	-0.12 to 0.04	Sire component of variance	Gunnes and Gjedrem (1978)
Atlantic salmon	% smolting at 1 year	-0.04 ± 0.09	Sire component of variance	Refstie *et al.* (1977)
Guppy	Lateral line scale count	-0.57 ± 0.22 to 1.14 ±0.80	Sire component of variance	Shami and Beardmore (1978)

The resemblance between parent and offspring could be measured by two ways (1) by regression of offspring on parents, or (2) by correlation between parent offspring.

Measuring the regression of offspring on parent is straightforward, if the number of offsprings obtained from each parent is constant. However, in most animal husbandry data, all the parents do not produce equal number of offsprings. In computing regression with variable number of offspring per parent, the problem of weighing these numbers arises. The two most commonly used practices are : (1) repeating parents' record with each record of offspring, (2) averaging all the offsprings of a parent, and to regress each average on the appropriate parent record. The former practice would be valid if the correlations among the offspring of a parent were to be zero, whereas the latter would be valid if the correlation among the members of each progeny group were to be one. Obviously, the real situation in most animal husbandry material is intermediate to these two extremes, although usually nearer to former (Kempthorne and Tandon, 1953).

Heritability estimates can also be obtained by regressions of offsprings on dam, sire and mean parent. All these heritabilty estimates are almost unbiased in a narrow sense, because they include only a little epistatic variation and no dominance variation. However, when maternal effect cannot be ignored, then, regression of offspring on sire estimate would be more unbiased, as compared to others, as it remains unaffected by any maternal effect. This estimate, however, is less commonly used because of the lesser degrees of freedom usually available for it. Moreover, it is not be available for sex limited traits.

Further, these estimates are free of environmental sources of coyariance, as parent and offsprings are usually measured over different periods and they are also not biased by selection of parents. This is because when, as a result of selection, the variance among the parents get reduced, the covariance also decreases proportionally, so that regression of offspring on parent remains unaltered. The precision of such estimates, however, is reduced (Jain, 1982) and they are least affected by system of mating (Reeve, 1953, 1955 and Wilson *et al.* 1966).

Heritability estimates from regression of offspring on parents reported for various aquatic organisms are presented below:

Kincaid (1972) has arrived at heritability values ranging from 0.26 to 0.29 for the body weight of rainbow trout on 150^{th} day of age.

McLaren (1976) estimated heritability of adult size in copepods using parent offspring data. He estimated heritabilities from various combinations like regression of male offspring on mean parent, male offspring on male parent, male offspring on female parent, female offspring on mean parent, female offspring on male parent, female offspring on female parent at different temperatures. The lowest estimated heritability was - 0.63 for female offspring on male parent at 10°C temperature while maximum was 0.74 for male offspring on male parent at 15°C.

McLaren and Corkett (1978) estimated the heritability of body size in marine copepod *Pseudocalanus sp.* at 0.98.

Heritability estimates ranged from 0.04 to 0.10 for early growth in *Oreochromis niloticus* from regression of offspring on parents (Tave and Smitherman, 1980).

Brody *et al.* (1981) estimated the heritability of growth in carp at 47 % from parent offspring regression.

There are, however, no reports of heritability estimates using regression of offspring on parent for any of the traits in *Artemia*.

Realized heritability

Student (1954), who introduced the concept of realized heritability, defined it as "the ratio of cumulative response and cumulative selection differential", while Falconer (1954) defined it as "the regression of cumulative response on cumulative selection differential".

Hill (1971, 1972 a, b) showed that population size, selection intensity, number of generation of selection and the parameter themselves are the factors which influence the precision or variance of realized heritability estimates.

Pirchner (1983) proposed that when epistasis, dominance and common environmental effects are unimportant, heritabilities from sibs correlation should be similar to realized heritabilities, and heritability estimates from offspring parent regression should also correspond to realized heritability.

In general, this method of estimating heritability appears optimal. However, few epistatic combinations may be inherited in first few generations and in such cases, selection response will be larger in earlier than in later generations of selection. Selection responses, based on such epistatic gene combinations, are not static and when the selection ceases, the epistatic combinations disintegrate and

corresponding response disappears. Thus, it overestimates permanent selection response by this amount. Additionally, maternal effects can influence selection response, in both positive and negative directions (Pirchner, 1983).

Therefore, the realized heritability has the appeal of being very simple computationally and it is operationally useful in describing the response to selection.

There are, however, no reports of realized heritability estimates for any of the *Artemia* traits. Its studies in other aquatic animals are also very few and some of them are mentioned below.

Thien (1971) reported realized heritability of 0.10 in male and 0.16 in female for growth rate in *Tilapia mossambicus*.

In *O. niloticus*, the realized heritability for body weight was - 0.05, although selection was carried out for increased body weight (Teichert Coddington, 1983).

Bondari *et al.* (1983) obtained a realized heritability of 0.23 ± 0.05 in *Tilapia aurea*.

According to Bondari (1983), the realized heritability for body weight in tilapia was considerably lower (0.10) than heritability values estimated from sire or dam components of variance.

In Thai red tilapia, the realized heritability estimate were 0.17 for length and 0.19 for weight (Jarimopas, 1986).

Teichert Coddington & Smitherman (1986) have estimated the realized heritability at 0.10 for early rapid growth in *Tilapia nilotica*.

Realized heritability of eight month body weight of coho salmon reared in salt water were 1.22 ± 0.32 for odd year line and 0.81 ± 0.30 for even year line (Hershbergor, 1990).

Realized heritability over five generations of selection were 0.126 for males, 0.13 for females and 0.19 for combined sex in *O. aureus* for weight (Sanchez *et al.*, 1995).

Correlations

The association between two traits, that can be directly observed, is the phenotypic correlation. This may be due to genetic or environmental factors, or combination of both. Genetic correlation between two traits is defined as "the correlation between genetic effects that influence the two traits". Genetic correlation can also be defined as the "correlation of the breeding values", while the environmental correlation is the "correlation of environmental deviation together with non-additive genetic deviation". Genetic correlation estimates the extent to which two traits are controlled by the same gene.

The theory of genetic correlation has been discussed in detailed by Hazel (1943), Lerner (1950) and Falconer (1960). The genetic correlation between two traits may be due to linkage, pleiotropy or a combination of the two. The genetic association due to linkage appears to be important when base population is derived from a cross involving several lines. It is transient in nature and breaks down automatically when selection is conducted for several generations. Pleiotropy is the property of a gene, whereby it affects two or more characters simultaneously. Pleiotropy is the overall or net effect of all the segregating genes that affect both the characters. Some genes may increase both the characters,

while others may increase one but reduce the other. The former tends to cause positive correlation while the latter a negative one. If both the characters have low heritability, then the phenotypic correlation is determined chiefly by the environmental correlation. If they have high heritabilities, then the genetic correlation is more important.

The magnitude and direction of correlated response to selection, among other factors, depend upon the genetic correlation between the selected and unselected traits.

Genetic correlation estimates permits to predict the correlated response in the unselected traits due to selection for primary traits. However, as indicated by the work of Bohren *et al.* (1966), prediction of correlated responses to selection, beyond a single generation is, likely to be highly inaccurate without certain prior knowledge of magnitude and composition of the genetic covariance. This implies that, highly accurate estimate of genetic correlations within a population is necessary to accurately predict correlated responses, even for a single generation. Thus, genetic correlation estimates as such are of any real value, only when used in the population from which they are estimated. An average of genetic correlation estimates, from different populations, is probably of value only as an indicator of the expected genetic correlation between two traits.

Errors of genetic correlation estimated from variance and covariance analysis, have been discussed by Tallis (1959), Robertson (1959b) and Hammond & Nicholas (1972). Errors of phenotypic correlation have been discussed by Goulden (1962). If genetic correlation and heritabilities are estimated from same

set of data, the error of the former is likely to be larger than that the latter (Pirchner, 1983).

Like the heritabilities, there are no reported studies of the genetic and phenotypic correlations among various traits in *Artemia*. These studies in aquatic species are limited to rainbow trout, salmon and common carp, and they indicate a very high and positive correlation between the body length and weight in them.

Wohlforth and Moav (1972), while studying the growth of seven groups of common carp at different periods, found a very high correlation ($r = 0.97$) between initial weight and growth during fall. However, they recorded a negative correlation ($r = -0.10$) between initial weight and weight gain during winter.

The genetic correlation between length and weight, of Atlantic salmon, was estimated to be 1.00 by Refstie & Steine (1978).

In rainbow trout also the genetic and phenotypic correlations between weight and length at one year age were very high *viz.*1.02 and 0.93 respectively (Refstie, 1980). Similarly, the genetic and phenotypic correlations estimated by Gunnes & Gjedrem (1981) were also found to be very high (0.98 and 0.88 respectively). Refstie & Steine (1978), Gunnes & Gjedrem (1978) and Refstie (1980) postulated that these two traits are largely controlled by same gene.

Phenotypic and genotypic correlations between growth and fecundity of rainbow trout were studied by workers like Gall (1975), Gall & Gross (1978), Haus (1984) and Halseth (1984). They observed that female body weight is correlated with egg size, egg volume and egg number.

Response to selection

Lush (1945) linked selection to the architectural process for creating a building of original design from already available material. Animal breeders define their design in terms of a desired phenotype and their building materials are alleles distributed among the genomes of individuals in the population, which qualitatively or quantitatively condition the expression of their phenotype. Selection does not create new alleles. It merely expedites the propagation of favoured allelic combinations and promotes the progressive elimination of those with less favourable effects.

Lerner (1958) defined selection as "non-random differential reproduction of genotypes". It is a process in which certain individuals in a population are allowed to reproduce the next generation while others are prevented from doing so. The primary objective of the selection is to change the gene frequency in the desirable direction. Selection in the quantitative traits results in the change of population mean.

Response to selection may be defined as the difference between the mean phenotypic values of the offspring of the selected individuals and that of the paternal generation from which the individuals were selected. The expected rate of improvement from selection depends upon selection intensity, degree of heritability of the trait under selection and generation interval (Dickerson, 1951). However, Dickerson (1955) observed that expected genetic change was somewhat greater than realized genetic change for the survivors. He used the term genetic slippage to describe the situation where the expected genetic gain is found to be greater than realized ones. He concluded that non-additive genetic effects,

included in the estimates of genetic parameters, would be a consistent cause of overestimation of expected response to mass selection.

The theoretical model and consequences of selection for metric traits have been discussed by Griffing (1960, 1962) under the assumption of a constant, environment. When the environment is constant from one generation to the other, the response to selection following 'n' cycles of selection should be equal to 'n' times the selection intensity times the heritability. However, it is seldom possible to have a constant environment over a long period of time and as such, the generation means remain confounded with the environmental effects. This makes it difficult to assess the effectiveness of selection and to know how much of the improvement is due to selection and how much due to progressive change in the environments. In order to overcome this difficulty and to measure the environmental trend during the course of selection, use of a random bred control population was suggested by King *et al.* (1959) and Gowe *et al.* (1959).

Marks (1978) concluded from his selection experiments that major genes were the first to be influenced by selection, followed by the additive action of minor genes in the later stages of selection programme. Due to this reason, response to early generations of selection are expected to be greater than those in the later generations.

The difference between the mean phenotypic value of the selected parents and the mean of the population from which they were selected is called the selection differential. It is the measure of selection pressure actually applied to bring about a change in the selected trait. Selection differential expressed in the standard deviation unit of the selected trait is known as intensity of selection.

Clayton *et al.* (1957) suggested that the realized response was below the expected response at lower intensities of selection but at higher selection intensities, there is close agreement between the expected and realized genetic gains. Robertson (1960) showed that total response was maximized when about half of the population were selected as parents for the next generation.

Falconer (1960) distinguished between the expected and the effective selection differentials because, in practice the individual parents do not contribute equally to the offspring generation. The major factors contributing towards the differences between expected and effective selection differentials are the differential rate of egg production among parents, fertility and hatchability and survival of progenies. The expected selection differential refers to the mean phenotypic deviation of the parents as stated above. The effective selection differential on the other hand, is the weighed mean deviation of the parents, the weight being given to each parent or pair of parents proportionate to their contribution to the next generation. By weighing the selection differential, one can measure the joint effects of natural and artificial selections. A comparison of weighed (effective) and unweighed (expected) selection differential, therefore, may be used to find out the effect of natural selection during the course of artificial selection.

Response to individual mass selection

Individual selection, sometimes referred to as mass selection, is the simplest method of selection, which involves choosing of the individuals to become parents of the next generation, based on their own phenotypic

performance. Individual selection is used to improve the performance of highly heritable traits.

However, there are no reports on the selective breeding of *Artemia*. Although, some attempts have been made on finfishes, the crustaceans remained rather neglected as far as genetic improvement through selective breeding is concerned.

An account of artificial selection experiments that have been undertaken in certain aquatic organisms are presented here under:

Hayford & Embody (1930) reported successful improvement of growth rate in salmonids by selection. Riggs and Sneed (1959) and Dollar & Katz (1964) reported improved growth in the rainbow trout through selection.

An early attempt for artificial selection in rainbow trout was made by Lewis (1944), who reported positive response in early spawning, egg number and yearling weight.

Donaldson & Olson (1957) reported significant improvement in growth rate, egg production and age of spawning in the rainbow trout *Salmo gairdneri* after 23 years, involving 7 - 10 generations of individual selection.

Significant response to individual selection for early sexual maturity has been reported in chinook salmon by Donaldson & Menasveta, 1961.

Selection experiments conducted by Kincaid *et al.* (1977) for growth in rainbow trout yielded a gain of 30 % over the three generations of selection.

The gain in body weight of Atlantic salmon as reported by Gjedrem (1979) was 7.7 % per year and 30 % per generation.

In oysters, the total gain in growth reported were 23 % (Newkirk & Haley, 1982) and 16.8 % (Newkirk & Haley, 1983).

In channel catfish, grown in earthen ponds, individual selection for body weight carried out by Dunham and Smitherman (1983) resulted in a gain of 16 % in the first generation itself.

Mallet *et al.* (1986) reported that the per cent mean change in larval shell length of the mussel *Mytylus edulis* was 4.7% per generation, with a selection intensity of 5 %.

Mass selection for grisle length in Atlantic salmon *Salmo salar* by Friars *et al.*, (1990) yielded a selection differential of 1.52 standard deviation or 6.7 cm and gains of 0.57 standard deviation on an index scale in progeny. The selected stock was reported to yield an average of 5744 eggs per female as compared to 4430 by the control.

Hershberger *et al.* (1990) recorded that body weight of coho salmon after 8-month rearing in saltwater increased from 239.0 gm to 432.5 gm after five generations of selection of odd year line and from 296.2 gm to 666.7 gm in the fifth generation of even year line. An increase in body weight was also observed in freshwater phase. The odd year line increased from 14.6 gm to 19.2 gm and even year line increased from 17.6 gm to 23.8 gm in freshwater phase. A weight gain of 6.4 - 7.0 % per generation was recorded for seven month in freshwater phase. However, 8 month saltwater weight showed an average weight gain of 10.15 gm per generation.

Toro & Newkirk (1991) reported a significant response to selection for decreased shell length in *Oreochromis chilensis*.

Lack of response or weak response to mass selection has been reported in a number of selection experiments in a variety of fishes. Ryman (1973) reported a weak response to within family selection in the guppy *Lebistes reticulatus*, where mass selection had been ineffective earlier. Kinghorn (1983) reported no response to selection for high growth in common carp. Hulata *et al.* (1986) reported that two generations of mass selection for growth rate in *Oreochromis niloticus* (Ghana strain) did not reveal any improvement over that of original base population.

Asymmetrical response in males and females have been reported by many workers. In caged channel catfish, gain for 40 week body weight was 8 % and 29% for male and female respectively (Bondari, 1983). From fourth generation of selection in Mosquito fish, weight gain of 12 % in male and 19 % in female has been reported by Busack (1983). From the five generations of individual selection for body weight in *O. niloticus*, Sanchez (1995) reported that the average genetic gains were 25.6 g, 11.2 g and 17.7 g in male, female, and control line respectively.

Bi-directional mass selection

A differential response to bi-directional selection has been reported by many workers, although, selection was initiated from the same base population

Moav & Wohlfarth (1976) reported a lack of response to within spawn selection for high growth rate in carps, over five generations, but they indicated a relatively strong response to selection for slow growth rate in first three generations.

Selection for body weight in tilapia *O. niloticus* was carried out by Abella *et al.* (1986). He reported that the high body weight line was 18% heavier than the contemporaries selected for low body weight.

Bondari (1986) observed asymmetrical response in channel catfish to bi-directional selection for 40 weeks body weight and total length. In the first generation, the downward line did not respond to selection while the response in the upward direction was 72 to 78 % greater than control for body weight and 17 to 18 % for total length. In the second generation, the observed responses for body weight and total length were 17.0 and 4.2 % greater than control in upward direction, and 44.2 and 16.3 % in downward direction.

In a bi-directional mass selection study in U.S. red tilapia, Behrends *et al.* (1987) found no response to selection for high body weight, but the response to selection for low body weight was significant.

Huang & Liao (1990) reported that brood tilapia from high body weight, low body weight and control lines were significantly different in body weight and total length.

Rochetta *et al.* (1996) observed from the individual selection for second month body weight in guppy that while the down line did not respond to bi-directional selection, the up line responded positively.

Realized responses, many a times reported to be lower than the predicted responses, are due to V_D and V_I effects, changes in the environment (V_E & $V_{G \cdot E}$), as well as sampling error resulting from working with a small population (Tave, 1986)

Correlated response

When selection is practised for any particular trait, changes are observed in some of the unselected correlated traits, along with change in the trait under selection. This change in unselected traits is called correlated response. It may result from genetic effects and/or environmental influences. Falconer (1960) derived a formula to quantify the correlated responses and Harvey & Bearden (1962) presented a procedure for calculation of the expected correlated change in standard deviation units, when direct selection was practised for another trait.

Yamada (1965) suggested that expected secondary selection differential in the unselected traits, when selection was conducted for a particular trait, was equal to the selection differential of selected trait multiplied by the phenotypic regression coefficient of correlated traits on the selected trait, only if selected and unselected traits were correlated with each other, and the two variables were normally distributed.

Freeden (1984) stated that if correlated responses prove undesirable, they may eventually nullify the improvement being sought in net productive merit and thus, impose a practical selection limit. Correlated responses may reflect multiple action of one or very few genes. Correlated responses may also reflect changes in some endocrine function that has a key role in producing the phenotypes desired from selection. For example, the pituitary function, because of its profound influence on the physiology of growth, may be the underlying object of phenotypic selection for growth rate. In such cases, selection for growth will have far reaching implications in respect to all developmental functions mediated by pituitary secretions. Another cause of correlated responses is the fact that

specific individuals, designated by selection for breeding use, contribute a random half of their entire genome to each of their progeny. The transmitted genes, even through totally correlated with the object of selection, may become fixed due to chance alone and may lead to an apparent association among the traits. The likelihood of such fixation has an inverse relation with population size.

Direction of correlated response in the unselected traits is generally same as that of selected traits, if both of them have a positively genetic correlation. A negative genetic correlation will, however, reverse the direction of correlated response. The magnitude and direction of correlated response to selection, among other factors, depend upon the genetic correlation between the selected as well as unselected traits. Like the direct responses, there are no reports of the correlated response pertaining to *Artemia*.

Ricker (1980 a, b) reported a correlated response of age at sexual maturity in cham and chinook salmon. The result indicated a positive genetic correlation between age of maturity and growth rate in cham salmon but a negative correlation in chinook salmon.

As per Gall & Gross (1978) the egg volume is the principle determinant of egg number and body weight has a strong positive influence on the egg volume in rainbow trout.

Haus (1984), while working on the rainbow trout, found a small negative genetic correlation between egg volume and body weight, implying that selection for higher body weight would result in a correlated reduction of egg volume.

Gjerde & Gjedrem (1984) studied the genetic correlation between age and body weight in Atlantic salmon and rainbow trout. While they observed a

negative genetic correlation of high magnitude of (-0.52) between body weight and age in Atlantic salmon , the magnitude of correlation in rainbow trout was lower (-0.11). Thus, it can be expected that, when selection is practised for improvement in body weight, a correlated response in the form of early maturity shall also be obtained. The magnitude of this correlated response is more in Atlantic salmon, as compared to rainbow trout, by virtue of the high a negative correlation in the former.


MATERIALS
&
METHODS

MATERIALS AND METHODS

Experimental material and setup

Base population

Artemia franciscana (Kellogg, 1906) from Great Salt Lake, Utah was used for conducting experiments during the present investigation. Base Population was raised by hatching the cyst of San Francisco Bay Brand of Inve Aquaculture, Inc, (batch no. 425 G, 06345).

Hatching and management practice

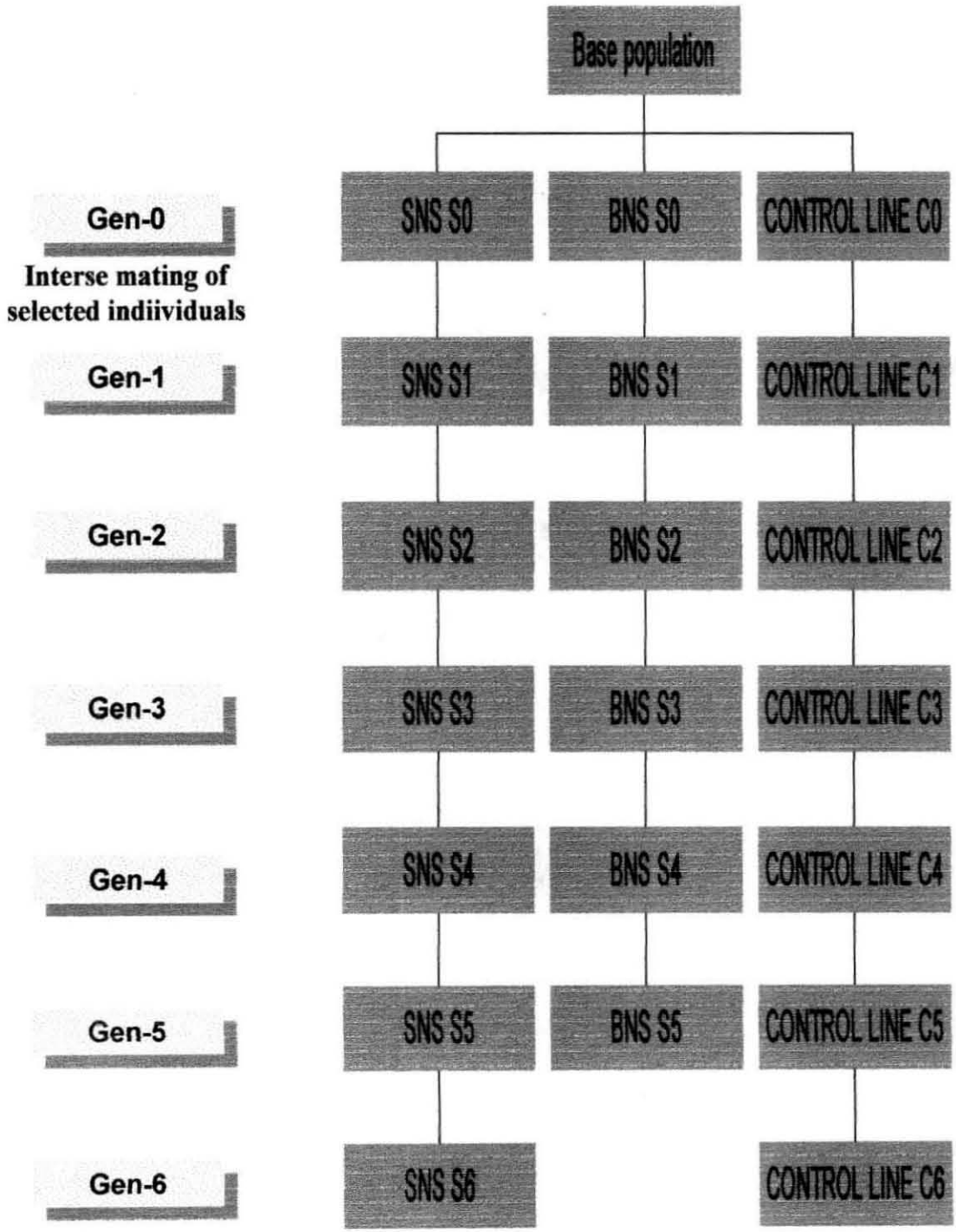
The cyst was incubated in 30 ppt seawater at the rate of 2.5 g /litre in a measuring cylinder. The pH of the seawater was 8.2 and temperature 30° C. Cyst was placed for incubation at 14.00hrs (02.00 p.m.), so as to ensure proper illumination during the initial incubation period. Continuous circulation of cyst in the water column was ensured by use of an aerator throughout the incubation period of 24 hours. The cysts hatched into free swimming nauplii on the next morning at 08.00 a.m. The aeration was then stopped and measuring jar was covered with black cloth. Nauplii were allowed to settle at the bottom of the cylinder and then siphoned out into a 1-litre beaker from the bottom of measuring cylinder with a 3 mm siphoning tube. From this beaker, nauplii were once again siphoned out into another 1-litre beaker so as to separate out unhatched cysts.

The nauplii thus collected were transferred to a 12-litre plastic basin containing 4 litres of 35 ppt seawater. Salinity level was gradually raised to 90

ppt by adding filtered saturated brine, prepared by dissolving the crude salt in 35 ppt sea water. The reproductive output of *Artemia* is found to be optimal in this medium i.e. 90 ppt (Bowen, 1962; Browne, 1980, 1982). Initially, nauplii were stocked at the rate of 20,000 no/ litre in 4 litres of seawater as suggested by Dhont *et al.*, (1993). The volume was then progressively increased up to 10 litres on the 6th day by adding 1 litre of 90 ppt sea water everyday. *Artemia* were fed as per diet (3) of Alejandro *et al.* (1995), with little modification (20 g baker's yeast + 0.5 g *Spirulina* powder +1.8 g ml cod liver oil). Every day, 10 % water was siphoned out with faeces and remainder food, after cleaning the basin carefully with hand. Siphoned out water was replenished with an equal volume of 90 ppt brine solution. Salinity of the culture media was checked everyday using refractometer, and was maintained at 90 ppt. On attaining sexual maturity, the individuals were divided into three groups, and designated as SNS, BNS and Control line respectively.

As soon as the males started clasping the females to form pairs, sixty-one pairs were picked up, and each pair was then kept in a 200 ml bottle containing 90 ppt sea water. They were fed with the same food as mentioned earlier. Bottoms of the bottles were cleaned every alternate days after carefully removing the breeders along with the supernatant water. After cleaning, the animals were placed back into the original bottle along with the same water. Bottles were examined twice a day, during mornings and evenings, for the release of nauplii. The collected nauplii were maintained individually in 50 ml bottles and fed with the same feed as mentioned above. On the 3rd, 6th and 9th days, the rearing bottles were cleaned and water was changed.

Fig-1. Schematic representation of Individual selection programme



Selection Programme

Method of selection followed for picking up the desirable individuals to become the parent of the next generation was Mass selection (individual selection) and the trait under selection was the naupliar size (length in μm). Bi-directional mass selection was practiced with the aim of developing two divergent stocks.

For this purpose, the base population was divided into three equal parts to be designated as Small Naupliar Size (SNS) line, Big Naupliar Size (BNS) line, and Control line. The criteria of selection were smaller naupliar size in SNS line, larger naupliar size in BNS line and no selection was practiced in control line. Schematic representation of selection programme is presented in Fig 1.

Selection programme in the SNS line was initiated by picking up sixty one pairs from base population of SNS group and keeping each pair in separate bottles for releasing nauplii. Ten nauplii from each of the 61 pairs of SNS constituted the S_0 generation of the SNS line. Individual data on the various traits, as listed in the Table 2 & Table 3 were recorded from them. On the 9^{th} day, all individuals selected from the S_0 generation on the basis of smaller size at naupliar stage were kept as pairs in separate bottles to facilitate mating. Ten progeny from each of these pairs constituted the first selected generation (S_1) of SNS line. This process of selection and breeding was repeated, till the 6^{th} selected generation (S_6) of SNS was produced. Recording of data, on the traits under study, was carried out individually from each animal in every generation.

The selection and breeding in the second group (BNS) was also carried out as outlined above, but with the difference of selecting bigger nauplii in place

Table 2. Traits measured in both males and females of each generation from all the lines before pairing.

Sr. No.	Trait measured
1	Nauplier size (length)
2	Length on 3 days of age
3	Length on 6 days of age
4	Length at sexual dimorphism
5	Age at sexual dimorphism

Table 3. Traits measured in females in each generation from all the lines after pairing.

Sr. No.	Trait measured
1	Age at first offspring laid
2	Length at first offspring laid
3	Number of offsprings in first brood

of smaller nauplii, and the selection was practiced till the 5th selected generation (S5 of BNS) was available.

The control line, which originated from the third division of the base population, was also regenerated along with each of the selected generation but without any selection. Breeders were picked up at random. The individuals of the control line were maintained similar to those of the selected lines. Data on the naupliar size (i.e., trait under selection) only was recorded from the control population.

Numbers of pairs mated in each generation of the different lines are given in Table 4. The number of individuals measured for the traits under study are presented in Table 5 according to sex, line and generation.

Population size and inbreeding

The increase in the inbreeding coefficient per generation for the selected line was calculated by using the following formula (Write, 1931):

$$\Delta F = 1/8 N_m + 1/8 N_f$$

Where,

N_m = Number of male parents which had progeny surviving up to first reproduction.

N_f = Number of female parents which had progeny surviving up to first reproduction.

For the control line ΔF was calculated as per formula of Gowe *et al.* (1959) as under :

$$\Delta F = 3/ 32 N_m + 1/ 32 N_f$$

Table 4. Number of individuals measured according to sex, line and generation.

Line	Sex	Generations						
		S0	S1	S2	S3	S4	S5	S6
Lower	Male	239	223	246	226	102	95	116
	Female	255	195	275	202	154	190	118
	Total	494	418	521	428	256	285	234
Higher	Male	239	187	215	162	65	78	-
	Female	255	171	186	153	91	168	-
	Total	494	358	401	315	156	246	-
Control	Male	239	98	75	70	51	63	45
	Female	255	112	91	88	59	81	58
	Total	494	210	166	158	110	144	103

Table 5. Number of pairs mated in each generation according to line

Line	Generations						
	S0	S1	S2	S3	S4	S5	S6
Lower	61	55	63	50	39	39	30
Higher	61	43	48	37	26	33	-
Control	61	65	78	79	54	71	51

Expected increment in the inbreeding coefficient for the various lines are presented in Table 6.

Statistical analysis

Means and Standard error

The mean, standard error and coefficient of variation were computed for each trait using the following formulae.

$$\bar{Y} = \frac{\sum_{i=1}^{n} Y_i}{n}$$

$$S.E = \sqrt{S^2 / n}$$

$$C.V\ (\%) = \frac{S}{\bar{Y}} \times 100$$

Where,

$\bar{Y}$ = mean.

Y_i = measurement of a trait on i^{th} individual.

n = number of individual

$$S^2 = \frac{\sum Y_i^2 - \frac{(\sum Y_i)^2}{n}}{n - 1}$$

Table 6. Expected increase in inbreeding coefficient

Line	Generations							Cummulative ΔF	Average Δ F
	S0	S1	S2	S3	S4	S5	S6		
Lower	0.0041	0.0046	0.0040	0.0050	0.0064	0.0064	0.0083	0.0388	0,0055
Higher	0.0041	0.0058	0.0052	0.0068	0.0096	0.0076	-	0.0391	0.0065
Control	0.0041	0.0039	0.0032	0.0032	0.0046	0.0035	0.0049	0.0274	0.0039

Heritability

The heritability of the selected and unselected traits were estimated from full sib data and from regression of offspring on parent. Heritability for each line was initially estimated within sex and within generation. These estimates were then pooled over generations, within sex and line, to provide mean estimates. Realized heritability was also calculated for each line separately, within sex, from the regression of response on cumulative selection differential.

a) Heritability estimate from full sib data

The variance component analysis was used to estimate sire component of variance and heritability from full-sib correlation. The linear statistical model used was :

$$Y_{ik} = \mu + S_i + e_{ik}$$

Where,

Y_{ik} = Observation of the k^{th} progeny of the i^{th} sire

μ = Overall mean

S_i = Effect of i^{th} sire

e_{ik} = Random error attributed to individuals, assumed to be normally and independently distributed with mean zero and variance σ^2_e.

The degrees of freedom (D.F.), sum of squares (SS), mean sum of squares (MS) and expected sum of squares (EMS) used for estimation of heritability are given below:

Analysis of variance

Source of variation	D.F.	SS	MS	EMS
Between sires	S-1	SS_S	MS_S	$\sigma^2_W + K_1\sigma^2_S$
Between sire within progeny	n. - S	SS_W	MS_W	$\sigma 2_W$

Where,

S = Total number of sires

n. = Total number of progeny

K_1 = Average number of progeny per sire

σ^2_S = Sire component of variance

σ^2_W = Error variance component

Computational formula

Source of variation	Sum of squares	Mean squares
Correction terms (C.T.)	$\frac{Y_{..}^2}{n_i}$	–
Between sires	$\sum \frac{Y_i^2}{ni} - C.T.$	$MS_S = SS_S/S\text{-}1$
Progeny within sire	$\sum\sum Y_{ij}^2 - \sum \frac{Y_{i.}}{n_i}$	$MS_W = SS_W / n. - S$

Estimation of variance component and heritability

$$\sigma^2_W = MS_W$$

$$\sigma^2_S = \frac{MS_S - MS_W}{K_1}$$

$$h^2_s = \frac{2\,\sigma^2_S}{\sigma^2_S + \sigma^2_W}$$

The value of K_1 was calculated from the following formula:

$$K_1 = \frac{1}{S-1}\left[n. - \frac{n_i^{\,2}}{n.} \right]$$

Standard error of heritability was calculated as per Swinger *et al.* (1964) using following formula:

$$\text{S.E. } h^2_S = 2\sqrt{\frac{2\,(n.-1)\,(1-t)^2\,[1+(K_1-1)\,t\,]^2}{K_1^{\,2}\,(n.\,S)\,(S-1)}}$$

Where,

't' is interclass correlation.

$$t = \frac{\sigma^2_S}{\sigma^2_S + \sigma^2_W}$$

The heritability estimates were pooled over generations, within line and sex for selected and unselected traits, following the procedure of Enfield *et al.* (1966). The formula for pooling the estimate is as follows:

$$\text{Pooled } h^2 = \frac{\frac{h_0^2}{V_0} + \frac{h_1^2}{V_1} + \frac{h_2^2}{V_2} + \frac{h_3^2}{V_3} + \frac{h_4^2}{V_4} + \ldots + \frac{h_n^2}{V_n}}{\frac{1}{V_0} + \frac{1}{V_1} + \frac{1}{V_2} + \frac{1}{V_3} + \frac{1}{V_4} + \ldots + \frac{1}{V_n}}$$

$$\text{S.E. of pooled } h^2 = \frac{1}{\frac{1}{V_0} + \frac{1}{V_1} + \frac{1}{V_2} + \frac{1}{V_3} + \frac{1}{V_4} + \ldots + \frac{1}{V_n}}$$

Where,

h_0^2, h_1^2, h_2^2, h_3^2,h_4^2, ...,h_n^2 are the heritability of character in the corresponding generation S_0, S_1, S_2, S_3, S_4, ..., S_n

V_0, V_1, V_2, V_3, V_4, ..., V_n are the squares of standard error of corresponding heritabilities.

b) Heritability by regression of offspring on parent.

Heritability of the traits was estimated also from the regression of offspring on parent. Sire-Son and Dam-Daughter data were used for this purposes. Statistical model and computational formulas are as follows:

i) Statistical model

$$Z_i = \beta X_i + e_i$$

Where,

Z_i = Value of offspring of the i^{th} sire

Xi = Observation of the i^{th} sire

β = Regression Z on X

e_i = Error associated with Zi

ii) Computational Formulas:

$$\Sigma z^2 = \Sigma Z^2 - \frac{(\Sigma Z)^2}{N}$$

$$\Sigma x^2 = \Sigma X^2 - \frac{(\Sigma X)^2}{N}$$

$$\Sigma xz = \Sigma XZ - \frac{(\Sigma X)\ (\Sigma Z)}{N}$$

Where,

N = Number of parent offspring

$$\widehat{Cov}_{XY} = \frac{\Sigma xz}{N - 1}$$

$$b = \frac{\widehat{Cov}_{xz}}{\sigma_X^2} = \frac{\Sigma xz}{\Sigma x^2}$$

(because N - 1 is common to both numerator and denominator)

Heritability was estimated as under:

$$b_{op} = \frac{½\ Cov_{op}}{V_P} = ½\ h^2\ ;$$

$$h^2 = 2\ b_{op}$$

$$h^2 = 2\ \widehat{Cov}_{XY} / \sigma_X^2 = 2b$$

Standard error of heritability was calculated as per Klein *et al.*, 1973 using following formula:

$$S^2b = \frac{\Sigma z^2 - \frac{(\Sigma xz)^2}{\Sigma x^2}}{N - 2}$$

$$S.\ E.\ (b) = \sqrt{\frac{S^2b}{\Sigma x^2}}$$

$$S.\ E.\ (h^2) = 2\ S.\ E.(b)$$

Correlation

The genotypic and phenotypic correlations were estimated using variance and co-variance component analysis (Becker, 1975). The analysis of variance table, for estimating the variance component, was same as the one used for estimating heritability. The procedure for analysis of covariance is given below:

Analysis of variance

Source of variation	d. f.	M. C. P.	E. M. C. P.
Between sires	S - 1	MCP_S	$Cov_W + K\ Cov_S$
Between progeny within sire	n. - S	MCP_W	Cov_W

Computational procedure

Source of variation	S. C. P.	M. S. C. P.
Correction term (CT)	$\frac{X..\ Y..}{n.}$	-
Source of variation	$\sum_{i} \frac{X_i Y_{i.}}{n.} - CT$	$\frac{SCP_S}{S - 1}$
Between progeny within sire	$\sum_{i}\sum_{i} X_{ij}\ Y_{ij} - \sum_{i} \frac{X_{i.} Y_{i.}}{n_{i.}}$	$\frac{SCP_W}{n. - S}$

Estimation of covariance components:

$$Cov_W = MCP_W$$

$$Cov_S = \frac{MCP_S - MCP_W}{K}$$

Estimation of genetic correlation (r_G):

$$r_{G\ (SY)} = \frac{Cov_S}{\sqrt{Var_{\ s(x)}\ Var_{\ s(y)}}}$$

Estimation of phenotypic correlation (r_P):

$$r_{p\ (SY)} = \frac{Cov_S + cov_W}{\sqrt{Var_{\ S(X)}\ Var_{\ w(y)}}\sqrt{Var_{\ S(Y)}\ Var_{\ W(Y)}}}$$

Standard error of genetic correlation was obtained as per Robertson (1959b), using following formula:

$$S.\ E.\ (r_G) = \frac{1 - r^2_G}{\sqrt{2}} \sqrt{\frac{S.\ E.\ (h^2_{\ X})\ S.\ E.\ (h^2_{\ Y})}{h^2_{(X)}\ h^2_{(Y)}}}$$

Standard error of phenotypic correlation was obtained as per Goulden (1962), using the following formula:

$$S.\ E.\ (r_P) = \sqrt{\frac{1 - r^2_P}{n - 2}}$$

The genotypic and phenotypic correlations among the various traits were estimated for each line, sex-wise and generation-wise, and then pooled over generations as per Enfields *et al.* (1966). The procedure involved is same as the one described for heritability, except that the heritabilities were replaced by the respective correlation coefficients.

Selection differentials

The expected selection differential was calculated as the difference between the mean of the selected individuals and mean of population, before selection, from which individuals were selected. The effective selection differential was calculated by weighing each parent by the number of its offspring.

The effect of natural selection was calculated from the ratio of effective selection differential to expected selection differential (Falconer, 1960).

Standardized selection differential (Intensity of selection)

$$i = \frac{\text{Effective selection differential}}{\text{Phenotypic standard deviation}}$$

Since the selection was applied in both the sexes, the value of intensity of selection (i) was estimated as the means of the two sexes i.e. $i = ½ (im + if)$ (Falconer, 1981).

Realized response to selection

Response to selection was calculated both at genetic and phenotypic levels. Realized phenotypic response per generation (mean phenotypic response) for the selected trait (naupliar size) was estimated within sex for each line separately, from the regression of generation mean on generation number.

Realized genetic gain (ΔG) per generation was estimated in a similar manner, but using generation means of selected lines (Corrected for control deviation). Estimation of generation mean, corrected for control deviation, was done by using the formula:

$$\Delta G = (S_n - C_n) - (S_0 - C_0)$$

Where,

S and C represent the selected and control lines respectively while subscripts represent the generation. Environmental effects between generations were corrected by taking mean difference between selected and control lines and assuming that environment has almost similar effect on them.

The regression (b) of generation means (Y) on generation number (X) was calculated as follows.

$$b_{yx} = \frac{\Sigma XY - \frac{\Sigma X \, \Sigma Y}{n}}{\Sigma X^2 - \frac{(\Sigma X)^2}{n}}$$

Where,

Y = Mean value of the trait under selection

X = Generation number

n = Number of paired observations

The standard error of the regression was calculated as per the formula given below:

$$S.E.(b) = \sqrt{\frac{\left[\Sigma Y^2 - \frac{(\Sigma Y)^2}{n}\right] - b\left[\Sigma XY - \frac{(\Sigma X)(\Sigma Y)}{n}\right]}{n-2\left[\Sigma X2 - \frac{(\Sigma X)^2}{n}\right]}}$$

The coefficient of regression estimated using the above formula was tested for its significance using the following formula of 't' test:

$$t = \frac{b}{S.E\ (b)} \quad \text{with } (n-2) \text{ degrees of freedom,}$$

Where there are n pairs of observations.

Predicted response to selection

The expected genetic response per generation was calculated for each line separately, within sex, as per the procedure described by Falconer (1960). The following formula was used for prediction of response.

$$\text{Response } (R) = i\ \sigma^2_p\ h^2$$

Where,

R = Average predicted response per generation

i = Average intensity of selection

$\sigma^2 p$ = Phenotypic standard deviation of the trait under selection

h^2 = Pooled heritability of selected trait

Pooled heritability was used for prediction of response since it is supposed to be more accurate than individual generation estimates (Kinney and Shoffner, 1967).

Correlated response to selection

The estimate of mean correlated response per generation was obtained by regressing the mean value of unselected trait of every generation on the generation number. The expected response in the correlated trait Y, due to selection on trait X, was calculated as per Falconer (1981), using following formulae:

$CR_Y = i\ h_X\ h_Y\ r_A\ \sigma_{pY}$

Cry = Expected response in the correlated trait (Y) due to selection of trait X.

i = Intensity of selection

h_X, h_Y = Square root of heritabilities of selected (X) and unselected (Y) traits .

σ_{pY} = Phenotypic standard deviation of unselected trait (Y).


RESULTS

RESULTS

1.0 PHENOTYPIC PARAMETERS.

The length of the freshly hatched nauplii within the base population varied from 381.8000 μm to 564.4000 μm in males and 398.4000 μm to 572.7000 μm in females. The mean naupliar length was 486.9912 ± 2.1136 μm in males and 490.5754 ± 1.8157 μm in females. The mean length on 3 days of age were 1.8679 ± 0.275 mm and 1.8712 ± 0.0270 mm for males and females respectively. Mean values for the length recorded on the 6^{th} day were 4.1005 ± 0.0754 mm in males and 4.2990 ± 0.0793 mm in females. Age and length at sexual dimorphism were 5.8861 ± 0.0663 days and 3.8004 ± 0.0238 mm respectively in males and 5.9766 ± 0.2043 days and 3.9053 ± 0.2740 mm in females. Age and length at the time of laying the first offspring were 16.00 ± 0.2259 days and 10.0888 ± 0.854 mm respectively. The total number of offsprings laid in the first brood was 53.5696 ± 1.3675. Phenotypic parameters of *A. franciscana* within the base generation are presented in Table 7.

2.0 GENETIC PARAMETERS

2.1 HERITABILITY OF SELECTED TRAIT

Heritability of naupliar length was estimated from the regression of progeny values on parent and also from the analysis of variance of full sib data sex-wise, for each generation. These estimates are presented in Table 8 and 9.

Table 7. Phenotypic parameters of Artemia *franciscana* (base generation).

Sr. No	Traits	Mean values	
		Male	Female
1	Naupliar length (µm)	486.9912 ± 2.1136	490.5754 ± 1.8157
2	Length on 3 days of age (mm)	1.8649 ± 0.0275	1.8712 ± 0.0270
3	Length on 6 days of age (mm)	4.1005 ± 0.0754	4.2990 ± 0.0793
4	Length at sexual dimorphism (mm)	3.8004 ± 0.0238	3.9053 ± 0.0274
5	Age at sexual dimorphism (days)	5.8861 ± 0.0663	5.9766 ± 0.2043
6	Length at first offspring laid (mm)	-	10.0888 ± 0.2259
7	Age at first offspring laid (days)	-	16.0000 ± 0.2259
8	Number of offspring in first brood	-	53.5696 ± 1.3675

Table 8 Heritability estimates for naupliar length in SNS and BNS lines by parent-offspring regression.

Generation	Heritability ± S. E.			
	SNS		**BNS**	
	Male offspring on male parent	Female offspring on female parent	Male offspring on male parent	Female offspring on female parent
0	0.5851 ± 0.2153	0.3766 ± 0.1899	0.5851 ± 0.2153	0.3766 ± 0.1899
1	0.3770 ± 0.2305	0.3249 ± 0.2337	0.2558 ± 0.2097	0.0210 ± 0.2238
2	0.1836 ± 0.2460	0.6866 ± 0.2955	0.0760 ± 0.3120	0.3120 ± 0.3153
3	-0.1262 ± 0.3470	0.2989 ± 0.4299	0.6902 ± 0.4717	0.2186 ± 0.4781
4	0.4601 ± 0.4320	0.1162 ± 0.3817	1.1806 ± 0.5280	1.0798 ± 0.4993
5	0.1034 ± 0.6839	0.3857 ± 0.4384	1.3522 ± 0.2834	0.9488 ± 0.4454
6	0.3791 ± 0.3393	0.4577 ± 0.4577	-	-
Pooled heritability	**0.2123 ± 0.0766**	**0.3885 ± 0.1108**	**0.5777 ± 0.1154**	**0.3364 ± 0.1176**
b ± S.E.	-0.0317 ± 0.0480	-0.0073 ± 0.01083	0.2064 ±0.0854	0.1698 ± 0.0748

Table 9 Heritablity estimates for naupliar length in SNS and BNS lines from full sib analysis.

Generation	Heritability ± S.E.			
	SNS		BNS	
	Male	Female	Male	Female
0	1.4669 ± 0.0921	1.3877 ± 0.1001	1.4669 ± 0.0921	1.3877 ± 0.1001
1	1.4146 ± 0.1027	1.1054 ± 0.1426	1.0412 ± 0.1541	1.1672 ± 0.1442
2	1.1034 ± 0.1263	1.0561 ± 0.1246	0.9996 ± 0.1445	1.2382 ± 0.1338
3	1.1297 ± 0.1315	1.1099 ± 0.1422	1.2696 ± 0.1416	1.3709 ± 0.1302
4	1.2898 ± 0.1740	0.8401 ± 0.1768	1.2007 ± 0.2368	1.4979 ± 0.1441
5	1.3153 ± 0.1731	1.1078 ± 0.1479	1.1155 ± 0.2300	1.6253 ± 0.0895
6	1.3635 ± 0.1490	0.3928 ± 0.1955	-	-
Pooled heritability	**1.3256 ± 0.0474**	**1.1004 ± 0.0522**	**1.2580 ± 0.0583**	**1.4221 ± 0.0479**
b ± S. E.	-0.0115 ± 0.0279	-0.1141 ± 0.0365 **	-0.0288 ± 0.0435	0.0661 ± 0.0300*

* and ** indicates the significance of the b at P<0.001 and P<0.005 respectively.

As can be seen from the above tables, though the estimate showed variation from generation to generation, the estimates from b_{op} were of medium magnitude compared to the estimates from full sib data which were very high. The pooled estimates of heritability, which is considered to be more reliable than individual estimates, also exhibited a similar trend. The heritability estimates from regression of progeny on parent, pooled over the generations, were 0.2123 ± 0.0766 and 0.3885 ± 0.1108 for males and females of SNS line. The corresponding figures in BNS line were 0.5777 ± 0.1154 and 0.3364 ± 0.1176 respectively. While the heritability estimates from the sib data, pooled over generations, were 1.3256 ± 0.0474 and 1.1004 ± 0.0522 for males and females respectively in SNS line, the corresponding estimates in BNS were 1.2580 ± 0.0583 and 1.4221 ± 0.0479 respectively. Though, the standard errors associated with individual estimates were generally high, they were of lower magnitude in case of pooled estimates.

The regression of heritability estimates on generation numbers, which indicate the change in heritability over the generations, were of low magnitudes.

2.2 HERITABILITY OF UNSELECTED TRAITS

Heritability of all the correlated traits under study were estimated from both regression of the offspring on parent as well as from sire component of variance, resulting from the analysis of variance of full sib data.

Initially, heritabilities were estimated generation-wise, within sex and line. The male offspring was regressed on sire while female progeny was regressed on dams. The individual estimates varied from low to medium magnitudes. These individual estimates were pooled over generation and mean heritabilities were

estimated. Using the full sib data also, heritabilities were initially estimated sex-wise and line wise, for each generation and they were then pooled over the generations.

The two sets of heritability estimates are presented below for each of the correlated traits.

2.2.1 Length on 3 days of age

Heritability estimates from b_{op} for the length on 3 days of age of both SNS and BNS lines were of low magnitude in most of the cases. The pooled heritability estimates were also low except in BNS females where it was of medium magnitude. The estimates are given in Table 10. The pooled heritability estimates for males and females of SNS line are 0.1524 ± 0.1008 and 0.0206 ± 0.1146 respectively and corresponding values of BNS are 0.0264 ± 0.1476 and 0.4292 ± 0.1414. The heritability estimates from sire component of variance were of very high magnitude. All the estimated values of heritability exceeded normal limits. But the standard errors were of very low magnitude. The heritability estimates for males and females of SNS line were 1.3989 ± 0.0442 and 1.4762 ± 0.0384 respectively and corresponding values of BNS were 1.6580 ± 0.0349 and 1.5549 ± 0.0394. The heritability estimates from sire component of variance are given in Table 11.

2.2.2 Length on 6 days of age

Heritability estimates from b_{op} for the length on 6 days of age in both the lines were generally of low magnitude, with few exceptions, especially in females (Table 12). The pooled heritability estimates were also low, being 0.1110

Table 10 Heritability estimates for length on 3 days of age in SNS and BNS lines by parent-offspring regression.

Generation	Heritability ± S. E.			
	SNS		BNS	
	Male	Female	Male	Female
0	0.3272 ± 0.3651	0.1167 ± 0.3841	0.3272 ± 0.3651	0.1167 ± 0.3841
1	-0.0367 ± 0.1791	0.0754 ± 0.2416	0.3846 ± 0.3079	0.2208 ± 0.2553
2	0.3649 ± 0.2309	0.0054 ± 0.2689	0.2773 ± 0.4340	0.7167 ± 0.4279
3	0.3748 ± 0.2081	0.3921 ± 0.2250	0.1030 ± 0.3009	0.5656 ± 0.3180
4	-1.2492 ± 0.4398	0.4899 ± 0.5939	0.0717 ± 0.4385	-0.3061 ± 0.4680
5	0.6337 ± 0.4066	0.1743 ± 0.4015	-1.3157 ± 0.6860	1.1496 ± 0.3538
6	0.1213 ±0.3893	0.3435 ± 0.3223	-	-
Pooled heritability	**0.1524 ±0.1008**	**0.0206 ± 0.1146**	**0.0264 ± 0.1476**	**0.4292 ± 0.1414**

Table 11 Heritability estimates for length on 3 day of age in SNS and BNS lines from full sib analysis.

Generation	Heritability ± S. E.			
	SNS		BNS	
	Male	Female	Male	Female
0	1.3607 ± 0.1049	1.4797 ± 0.0890	1.3607 ± 0.1049	1.4797 ± 0.0890
1	1.3098 ± 0.1148	1.2159 ± 0.1328	1.4365 ± 0.1131	1.5804 ± 0.0890
2	1.2446 ± 0.1158	1.3806 ± 0.0977	1.7995 ± 0.0439	1.5938 ± 0.0848
3	1.4833 ± 0.0943	1.5125 ± 0.0965	1.4169 ± 0.1220	1.5138 ± 0.1079
4	1.5270 ± 0.1297	1.6130 ± 0.0907	1.4883 ± 0.1745	1.6665 ± 0.1032
5	1.3434 ± 0.1682	1.3332 ± 0.1258	1.4345 ± 0.1750	1.4713 ± 0.1170
6	1.5015 ± 0.1246	1.6081 ± 0.1014	-	-
Pooled heritability	**1.3989 ± 0.0442**	**1.4762 ± 0.0384**	**1.6580 ± 0.0349**	**1.5549 ± 0.0394**

Table 12 Heritability estimates for length on 6 days of age in SNS and BNS lines by parent-offspring regression.

Generation	Heritability ± S. E.			
	SNS		**BNS**	
	Male	Female	Male	Female
0	0.4965 ± 0.2466	0.0222 ± 0.2971	0.4965 ± 0.2466	0.0222 ± 0.2971
1	0.1548 ± 0.2178	0.4412 ± 0.3198	0.1997 ± 0.2236	0.5562 ± 0.3262
2	0.1063 ± 0.1953	0.2466 ± 0.1681	0.17660 ± 0.3009	0.0135 ± 0.2215
3	0.3761 ± 0.2678	0.2523 ± 0.1618	0.1030 ± 0.8544	0.0910 ± 0.3284
4	-1.4873 ± 0.8076	0.6415 ± 0.7159	0.6095 ± 0.3117	1.0176 ± 0.8112
5	-0.5578 ± 0.3082	0.0109 ± 0.2693	-0.0543 ± 0.07840	0.6623 ± 0.1982
6	-0.1516 ± 0.4417	0.7984 ± 0.3821	-	-
Pooled heritability	**0.1110 ± 0.1027**	**0.2541 ± 0.0923**	**0.1335 ± 0.0784**	**0.3232 ± 0.1137**

± 0.1027 and 0.2541 ± 0.0923 for males and females of SNS and 0.1335 ± 0.0784 and 0.3232 ± 0.1137 in BNS lines. The heritability estimates from sire component of variance form full sibs data are presented in Table 13, these estimates were of very high magnitude like that for the length on 3 days of age. The pooled heritability values in SNS line were 1.2757 ± 0.0499 and 1.4407 ± 0.0401 in males and females respectively. The corresponding values for BNS were 1.2615 ± 0.0565 and 1.3852 ± 0.0499 respectively.

2.2.3 Length at sexual dimorphism

The generation-wise heritabilities as well as pooled heritabilities for the length at sexual dimorphism estimated from b_{op} are given in Table 14. It can be seen from table that both the individual estimates and the pooled estimates were very low. The pooled estimates were 0.0133 ± 0.0836 and 0.0078 ± 0.0807 for males and females of SNS line and -0.1255 ± 0.0896 and $0.0772 \pm 0.0963$for males and females of BNS line. The heritability estimates for length at sexual dimorphism in SNS and BNS lines from full sib data are presented in Table 15. Most of the estimates were within the normal limits for heritability whereas the remaining one were slightly greater than unity. The pooled heritability for males and females were 0.8679 ± 0.0596 and 1.0264 ± 0.0534 respectively in SNS line, and 1.0221 ± 0.0643 and 1.0314 ± 0.0615 in BNS line. The standard errors estimated for heritabilities were of lower magnitudes.

2.2.4 Age at sexual dimorphism

The heritability estimates of the age (days) at sexual dimorphism in SNS and BNS lines by parent offspring regression were generally of low magnitude

Table 13 Heritability estimates for length on 6 days of age in SNS and BNS lines from full sibs analysis.

Generation	Heritability ± S. E.			
	SNS		BNS	
	Male	Female	Male	Female
0	1.2757 ±0.1138	1.3639 ±0.1027	1.2757 ±0.1138	1.3639 ±0.1027
1	1.2423 ±0.1216	1.5228 ±0.0940	1.3483 ±0.1250	1.4077 ±0.1160
2	0.9129 ±0.1365	1.1188 ±0.1202	1.3009 ±0.1206	1.1397 ±0.1430
3	1.1100 ±0.1329	1.2497 ±0.1298	0.8773 ±0.1714	1.1773 ±1.1537
4	1.5009 ±0.1353	1.6478 ±0.0838	1.6134 ±0.1393	1.6478 ±0.1081
5	1.0866 ±0.2653	1.1512 ±0.1445	0.4246 ±0.2408	1.3620 ±0.1333
6	1.5549 ±0.1140	1.6065 ±0.1019	-	-
Pooled heritability	**1.2757 ±0.0499**	**1.4407 ±0.0401**	**1.2615 ±0.0565**	**1.3852 ±0.0499**

Table 14 Heritability estimates for length at sexual dimorphism in SNS and BNS lines by parent-offspring regression.

Generation	Heritability ± S. E.			
	SNS		BNS	
	Male	Female	Male	Female
0	-0.1706 ±0.1519	-0.0437 ±0.1695	-0.1706 ±0.1519	-0.0437 ±0.1695
1	0.0177 ±0.3307	0.393 0±0.2480	0.024 ±0.3463	0.3611 v0.3788
2	0.0989 ±0.1682	-0.0021 ±0.1864	-0.2113 ±0.2395	0.0340 ±0.2011
3	0.2131 ±0.1705	0.0335 ±0.1498	-0.086 ±0.1448	-0.0225 ±0.1972
4	-0.3065 ±0.4235	0.4384 ±0.5439	-0.0865 ±0.4865	0.1921 ±0.7948
5	0.0834 ±0.3260	-0.4502 ±0.2533	-0.0826 ±0.5415	0.4805 ±0.2665
6	-0.1516 ±0.4417	0.0421 ±0.3125	-	-
Pooled heritability	**0.0133 ±0.0836**	**0.0078 ±0.0807**	**-0.1255 ±0.0896**	**0.0772 ±0.0963**

Table 15 Heritability estimates for length at sexual dimorphism in SNS and BNS lines from full sibs analysis.

Generation	Heritability ± S. E.			
	SNS		BNS	
	Male	Female	Male	Female
0	0.8830 ±0.1395	0.7900 0.1378	0.8830 ±0.1395	0.7900 ±0.1378
1	1.1491 ±0.1298	1.2516 ±0.1291	1.0844 ±0.1511	1.4174 ±0.1146
2	0.8361 ±0.1390	1.0802 ±0.1226	1.3740 ±0.1122	1.1664 ±0.1406
3	0.5141 ±0.1432	1.0719 ±0.1450	0.4565 ±0.1675	0.6089 ±0.1777
4	1.1781 ±0.1899	1.3837 ±0.1294	1.0893 ±0.2540	0.5548 ±0.2335
5	0.7405 ±0.2299	0.5910 ±0.1594	0.7367 ±0.2542	0.9924 ±0.1681
6	0.6676 ±0.2052	0.5751 ±0.2026	-	-
Pooled heritability	**0.8679 ±0.0596**	**1.0264 ±0.0534**	**1.0221 ±0.0643**	**1.03142 ±0.0615**

(Table 16) with the pooled estimates for males and females being 0.0172 ± 0.0890 and 0.1277 ± 0.0397 in SNS line, and 0.0783 ± 0.0387 and -0.0009 ± 0.0061 in BNS respectively. Heritability estimates for age at sexual dimorphism of SNS and BNS lines from full sib data were of medium to very high magnitude, though the standard errors were of low magnitudes like other correlated traits. The pooled estimates were 1.1049 ± 0.0520 and 1.1795 ± 0.0420 for males and females respectively in SNS line. The corresponding values of the BNS lines were 0.7940 ± 0.0523 and 1.3211 ± 0.0463 for males and females respectively. Individual heritabilities and pooled heritabilities from full sibs data are presented in Table 17.

2.2.5 Age at first offspring laid

The heritabilities from the parent offspring regression for age at the time of first offspring laid are given in Table 18. The estimates were of very low magnitude. The pooled estimates were 0.0881 ± 0.0842 and 0.1862 ± 0.0942 in SNS and BNS females. Heritability estimates from full sib data are given in Table 19. The estimates were of very high magnitude with low standard errors. The pooled estimates were 1.5833 ± 0.0506 and 1.8020 ± 0.0333 in SNS and BNS females respectively.

2.2.6 Length at first offspring laid

Heritability for length at first offspring laid as estimated from b_{op} varied considerably between generations from low to high values (Table 20), with pooled estimates being 0.3700 ± 0.1100 and 0.1304 ± 0.1441 in SNS and BNS lines respectively. However, pooled estimates of heritabilities from the sire

Table 16 Heritability estimates for age at sexual dimorphism in SNS and BNS lines by parent-offspring regression.

Generation	Heritability ± S. E.			
	SNS		**BNS**	
	Male	Female	Male	Female
0	0.3639±0.2542	-0.1011±0.2856	0.3639 ±0.2542	-0.1011±0.2856
1	-0.0325 ±0.1355	0.1617 ±0.1502	-0.0913 ±0.2290	0.3695±0.2209
2	0.0246 ±0.1658	0.1137 ±0.0430	0.0431 ±0.0412	-0.0014±0.0061
3	0.3950 ±0.4441	0.3783 ±0.3553	0.4986 ±0.7406	0.69385 ± 1.3891
4	-0.3669 ±0.7621	-0.1031 ±0.6349	0.51189 ±0.8801	1.3891±0.0295
5	-0.3605 ±0.3389	0.2825 ±0.2293	0.5324 ±0.1579	0.0265±0.1260
6	-0.1839 ±0.4735	0.7851 ±0.3823	-	-
Pooled heritability	**0.0172 ±0.0890**	**0.1277 ±0.0397**	**0.0783 ±0.0387**	**-0.0009 ±0.0061**

Table 17 Heritability estimates for age at sexual dimorphism in SNS and BNS lines from full sibs analysis.

Generation	Heritability ± S. E.			
	SNS		BNS	
	Male	Female	Male	Female
0	1.1311 ±0.1262	0.7793 ±0.1380	1.1311 ±0.1262	0.7793 ±0.1380
1	1.2987 ±0.1160	1.7522 ±0.5390	1.2110 ±0.1404	1.5467 ±0.0947
2	0.4121 ±0.1354	0.0434 ±0.0962	-0.0477 ±0.0962	0.0394 ±0.1495
3	0.7906 ±0.1463	0.7664 ±0.1570	0.5267 ±0.1707	0.8108 ±0.1769
4	1.4479 ±0.1460	1.4926 ±0.1124	1.7078 ±0.1096	1.7632 ±0.0763
5	0.8123 ±0.2272	0.9438 ±0.1574	0.1007 ±0.1948	1.3397 ±0.1363
6	1.5047 ±0.1240	1.7682 ±0.0641	-	
Pooled heritability	**1.1049 ±0.0520**	**1.1795 ±0.0420**	**0.7940 ±0.0523**	**1.3211± 0.0463**

Table 18 Heritability estimates for age at first offspring laid by females in SNS and BNS lines by parent-offspring regression.

Generation	SNS		BNS	
	Heritability	S.E.	Heritability	S.E.
0	0.0403	±0.1078	0.0403	±0.1078
1	-0.2377	±0.5198	-0.6758	±0.3672
2	0.0928	±0.1934	0.0270	±0.7872
3	-0.0059	±0.3450	0.4879	±0.5609
4	0.8828	±0.5146	0.2655	±0.8527
5	0.3314	±0.2857	1.5779	±0.2770
Pooled heritability	0.0881	±0.0842	0.1862	±0.0942

Table 19 Heritability estimates for age at first offspring laid by females in SNS and BNS lines from full sibs analysis.

Generation	SNS		BNS	
	Heritability	S.E.	Heritability	S.E.
0	1.1560	±0.1508	1.1560	±0.1506
1	1.6815	±0.0850	1.6985	±0.0926
2	1.7173	±0.0970	1.4238	±0.1969
3	1.4330	±0.2146	1.7074	±0.1646
4	1.6519	±0.1181	1.7395	±0.1258
5	0.4006	±0.3323	1.8969	±0.0404
Pooled heritability	**1.5833**	**±0.0506**	**1.8020**	**±0.0333**

Table 20 Heritability estimates for length at first offspring laid by females in SNS and BNS lines by parent-offspring regression.

Generation	SNS		BNS	
	Heritability	S.E.	Heritability	S.E.
0	0.3234	±0.2874	0.3234	±0.2874
1	-0.1471	±0.2626	-0.3766	±0.2732
2	0.3624	±0.4063	0.0338	±0.334
3	0.1268	±0.2071	-0.1127	±0.5613
4	0.5318	±0.3200	-0.3107	±0.8195
5	1.089	±0.2427	0.8786	±0.3329
Pooled heritability	**0.3700**	**±0.1100**	**0.1304**	**±0.1441**

component of variance from full sib data were of high to very high magnitude, being 0.7428 ± 0.0504 and 1.1141 ± 0.0456 for SNS and BNS females respectively. The generation-wise estimates for both the lines from full sib data are presented in Table 21.

2.2.7 Number of offsprings in first brood

Heritability for the number of offsprings in first brood was low to moderate magnitude in both the lines, excepting the third and fourth generations of SNS (Table 22). The pooled estimates were 0.3565 ± 0.1063 in SNS and 0.3311 ± 0.1046 in BNS. Heritabilities estimated from full sib data for the number of offsprings in first brood were of high to very high magnitudes (Table 23). The pooled heritability estimates were 1.2095 ± 0.0787 in SNS and 1.1450 ± 0.0829 in BNS.

2.3 CORRELATION BETWEEN SELECTED AND UNSELECTED TRAITS

Genetic, phenotypic and environmental correlation between the selected trait *viz.* naupliar length and other correlated traits like length on 3-days of age, length on 6 days of age, length & age at sexual dimorphism, age & length at first offspring laid and number of offsprings in first brood are presented below. The correlations were initially estimated within sex/ generation/ line basis and then pooled over generations for each line within sex.

2.3.1 Naupliar length and length on 3 days age.

The estimates of genetic, phenotypic and environmental correlation coefficients between naupliar length and length on 3-day age are presented in

Table 21 Heritability estimates for length at first offspring laid by females in SNS and BNS lines from full sib analysis.

Generation	SNS		BNS	
	Heritability	S.E.	Heritability	S.E.
0	0.6611	±0.1295	0.6611	±0.1295
1	0.6124	±0.1489	0.0906	±0.1589
2	1.2780	±0.0851	0.2256	±0.1456
3	-0.1103	±0.1286	1.5546	±0.0720
4	0.8671	±0.1485	1.3215	±0.1464
5	0.3571	±0.1498	1.2718	±0.1032
Pooled heritability	**0.7428**	**±0.0504**	**1.1141**	**±0.0456**

Table 22 Heritability estimates for number of offsprings in first brood by females in SNS and BNS lines by parent-offspring regression.

Generation	SNS		BNS	
	Heritability	S.E.	Heritability	S.E.
0	0.3404	±0.2202	0.3404	±0.2202
1	0.384	±0.2645	0.2676	±0.1652
2	0.4617	±0.1945	0.2527	±0.2766
3	-0.1221	±0.3262	0.2323	±0.6172
4	-0.1008	±0.4639	0.3511	±0.5925
5	0.6445	±0.276	0.5481	±0.2539
Pooled heritability	**0.3565**	**±0.1063**	**0.3311**	**±0.1046**

Table 23 Heritability estimates for number of offsprings in first brood by females in SNS and BNS lines from full sibs analysis.

Generation	SNS		BNS	
	Heritability	S.E.	Heritability	S.E.
0	0.7911	±0.1745	0.7911	±0.1745
1	1.3998	±0.1449	0.7991	±0.2633
2	0.9864	±0.2560	1.1200	±0.2659
3	0.9877	±0.3196	1.7474	±0.1439
4	1.3002	±0.2100	1.0084	±0.3579
5	1.4557	±0.1731	0.7518	±0.1885
Pooled heritability	**1.2095**	**±0.0787**	**1.1450**	**±0.0829**

Table 24. As can be seen from the table, the genetic correlations were mostly positive in direction and low to medium in magnitude in both the selected lines. The pooled genetic correlation values were 0.3277 ± 0.0208 in males and 0.4908 ± 0.0193 in females of SNS. The corresponding values in BNS were 0.3537 ± 0.0213 and 0.1528 ± 0.1528.

The phenotypic correlations were of lower magnitude and positive in most of the generations in male as well as females of both the lines. The pooled estimates of SNS and BNS males were 0.1688 ± 0.0281 and 0.1939 ±0.0320 respectively, whereas the corresponding values in females were 0.2740 ±0.0260 and 0.1494 ±0.0307. The environmental correlations were predominantly negative in most of the generations in males as well as females of both lines. The values of environmental correlation varied from -0.0083 to 0.4279.

2.3.2 Naupliar length and length on 6 days of age

The estimates of genetic correlation in males and females of both the lines were of low magnitude with negative values in few cases. The pooled genetic correlation estimates in males were 0.3023 ± 0.2310 and 0.2668 ± 0.0273 of SNS and BNS line respectively. The corresponding values in females were 0.2674 ± 0.0237 and -0.6121 ± 0.1255.

The phenotypic correlations also showed the same trend as genetic correlations. Pooled estimates of phenotypic correlations of males and females were 0.1560 ±0.0310 and 0.1584 ± 0.0262 respectively of SNS lines, whereas, the estimates in BNS lines were 0.1155 ± 0.0323 in males and 0.1255 ± 0 .0106 in females. The environmental correlations were of low magnitudes and fluctuated

Table 24 Genetic, phenotypic and environmental correlations between selected trait (naupliar length) and unselected trait (3-day length) in SNS and BNS lines.

Line	Generation	Male					Female				
		r_G	±S.E.	r_P	±S.E.	r_E	r_G	±S.E.	r_P	±S.E.	r_E
SNS	0	0.5680	0.0333	0.3411	0.0615	-0.5516	0.513	0.0343	0.3225	0.0597	-0.4575
	1	0.2492	0.0529	0.1489	0.0668	-0.2438	0.5198	0.0613	0.3764	0.0677	-0.3297
	2	0.0991	0.072	0.1177	0.0641	0.0457	0.2225	0.0613	0.2135	0.0592	0.1605
	3	0.0533	0.0607	0.0715	0.0666	0.0446	0.051	0.0638	0.1483	0.0708	0.4279
	4	0.0321	0.0756	0.0286	0.102	-0.0083	0.5238	0.0558	0.2727	0.0783	-0.5060
	5	0.3155	0.0817	0.2281	0.1026	-0.2122	0.4558	0.0629	0.3166	0.0692	-0.3964
	6	0.2629	0.0627	0.1788	0.0921	-0.2044	0.7995	0.0452	0.2551	0.0898	-0.3196
Pooled		**0.3277**	**0.0208**	**0.1688**	**0.0281**	-	**0.4908**	**0.0193**	**0.2740**	**0.0260**	-
BNS	0	0.568	0.0333	0.3411	0.0615	-0.5516	0.513	0.0343	0.3225	0.0597	-0.4575
	1	-0.0375	0.0762	0.0238	0.0743	0.1492	0.1363	0.0579	0.1235	0.0763	-0.0235
	2	0.1363	0.0412	0.1137	0.0684	-0.0549	0.3239	0.048	0.2089	0.0727	-0.3000
	3	0.3697	0.0598	0.2572	0.0766	-0.2733	0.3405	0.0514	0.2315	0.0792	-0.2643
	4	-0.1096	0.1062	-0.0223	0.1291	0.2124	-0.1129	0.0539	-0.0085	0.1072	0.2043
	5	0.5734	0.0753	0.326	0.1084	-0.6014	-0.3984	0.0394	-0.1709	0.0765	0.4876
Pooled		**0.3537**	**0.0213**	**0.1939**	**0.0320**	-	**0.1528**	**0.1528**	**0.1494**	**0.0307**	-

between positive and negative directions from generation to generation. The estimates for genetic, phenotypic and environmental correlation coefficients are presented in Table 25.

2.3.3 Naupliar length and length at sexual dimorphism

Pooled genetic correlations were positive in males as well as females of both the lines, although estimates for individual generations varied. The coefficients were of low to moderate magnitude, with the pooled estimates being 0.1782 ±0.0328 and 0.3315 ±0.3155 in males and females of SNS and 0.3315 ±0.0316 and 0.0740 ±0.3850 in BNS.

The phenotypic correlation coefficients were generally very low in both the sexes of both the lines. The pooled estimates of SNS were 0.1160 ±0.0228 and 0.1512 ±0.0267 in males and females respectively. The corresponding values in the BNS were 0.1512 ±0.0267 and 0.0529 ±0.0328. Environmental correlation varied in magnitude and direction from one generation to other. The estimates of genetic, phenotypic and environmental correlation between naupliar length and length at sexual maturity are given in Table 26.

2.3.4 Naupliar length and age at sexual dimorphism

Coefficients of genetic correlation between naupliar length and age at sexual dimorphism were mostly negative in males of both SNS and BNS lines. In females, the estimate fluctuated more frequently. The pooled genetic correlation coefficients were negative and of low magnitudes in both sexes of SNS line and males of BNS line. On the other hand, the pooled estimates in the females of BNS line were positive and high (0.7745 ±0.0108).

Table 25 Genetic, phenotypic and environmental correlations between selected trait (naupliar length) and unselected trait (6-day length) in SNS and BNS lines.

Line	Generation	Male					Female				
		r_G	S.E.	r_P	±S.E.	r_E	r_G	±S.E.	r_P	±S.E.	r_E
SNS	0	0.5610	0.0363	0.3377	0.0615	-0.5714	0.4879	0.0397	0.2738	0.0607	-0.5348
	1	0.0864	0.0592	0.0471	0.0675	-0.1017	0.0480	0.0630	0.0991	0.0728	0.2349
	2	0.1780	0.0896	0.1298	0.0640	-0.1183	0.3963	0.0669	0.2318	0.0590	-0.8922
	3	0.1543	0.0815	0.0827	0.6660	-0.1857	0.1627	0.0794	0.1102	0.0712	-0.1529
	4	-0.1570	0.0761	-0.0857	0.1017	0.1844	0.0809	0.0727	0.0935	0.0810	0.0816
	5	0.1175	0.1100	0.1633	0.1040	0.1385	0.1440	0.0896	0.1715	0.0719	0.4430
	6	0.2941	0.0578	0.1992	0.0918	-0.2378	0.0331	0.0713	0.0147	0.0769	-0.0586
Pooled		**0.3023**	**0.2310**	**0.1560**	**0.0310**	-	**0.2674**	**0.0237**	**0.1584**	**0.0262**	-
BNS	0	0.561	0.0363	0.3377	0.0615	-0.5714	0.4879	0.0397	0.2738	0.0607	-0.5348
	1	-0.0175	0.0828	0.0277	0.0743	0.1245	0.0331	0.0713	0.0147	0.0769	-0.0586
	2	-0.0424	0.0817	0.0109	0.0688	0.1446	0.3169	0.074	0.2089	0.0727	-0.3000
	3	0.0812	0.1037	0.1106	0.0788	0.0894	-0.1187	0.0776	0.0113	0.0814	0.4599
	4	-0.4188	0.0761	-0.1863	0.1268	0.6101	-0.5241	0.0407	-0.2589	0.1036	0.5693
	5	0.2742	0.2236	0.1002	0.1141	-0.4600	-0.8457	0.0148	-0.4127	0.0707	1.0027
Pooled		**0.2668**	**0.0273**	**0.1155**	**0.0323**	-	**-0.6121**	**0.1255**	**0.0106**	**0.3051**	-

Table 26 Genetic, phenotypic and environmental correlations between selected trait (naupliar length) and unselected trait (length at sexual dimorphism) in SNS and BNS lines

Line	Generation	Male					Female				
		r_G	S.E.	r_P	±S.E.	r_E	r_G	±S.E.	r_P	±S.E.	r_E
SNS	0	0.3306	0.0627	0.1664	0.0645	-0.4262	0.4086	0.0661	0.2327	0.0614	-0.2441
	1	0.1036	0.0633	0.0695	0.0674	-0.0592	0.0267	0.0815	0.0897	0.0728	0.4141
	2	0.2607	0.0909	0.1462	0.0639	-0.2724	0.3589	0.0711	0.1826	0.0596	-1.3181
	3	0.4319	0.1036	0.2091	0.0653	0.5926	0.3463	0.0819	0.1510	0.0708	-1.3043
	4	-0.2184	0.0993	-0.0847	0.1017	0.3899	0.0507	0.0989	0.0180	0.0814	-0.0834
	5	0.0713	0.1422	0.0600	0.1052	0.5026	0.1904	0.1293	0.1280	0.0723	0.0906
	6	0.0398	0.1294	0.0583	0.0935	0.1124	0.8287	0.0928	0.1987	0.0910	-0.1572
Pooled		**0.1782**	**0.0328**	**0.1160**	**0.0228**	-	**0.3315**	**0.3155**	**0.1512**	**0.0267**	-
BNS	0	0.3306	0.3306	0.1664	0.0645	-0.4262	0.4086	0.0661	0.2327	0.0614	-0.2441
	1	-0.0108	-0.0108	0.0209	0.0743	0.1269	-0.1628	0.0688	-0.0833	0.0767	0.2452
	2	-0.0812	-0.0812	0.0262	0.0688	0.3920	0.2393	0.0760	0.0609	0.0742	-0.7158
	3	-0.088	-0.0880	-0.0097	0.0793	0.2617	0.1332	0.1156	0.1386	0.0806	0.1380
	4	-0.4259	-0.4259	-0.1876	0.1268	0.6640	-0.8046	0.0502	-0.2212	0.1046	0.6320
	5	0.3505	0.3505	0.1685	0.1131	-0.4862	-0.3001	0.0621	-0.1283	0.077	2.0502
Pooled		**0.3315**	**0.0316**	**0.1512**	**0.0267**	-	**0.0740**	**0.3850**	**0.0529**	**0.0328**	-

The phenotypic correlation coefficients also showed a similar trend as that of genetic correlation coefficients but were of lower magnitudes. The pooled phenotypic correlation coefficients were very low and negative in direction excepting females of BNS line (0.0833 ± 0.0308). The environmental correlation coefficients did not present any definite pattern either in terms of direction or magnitude. The estimates were negative in all the generations excepting base and sixth generation females of SNS line. However, in males of SNS the estimates were positive except first, second and fourth generation. In BNS line, the estimates of environmental correlation coefficient have ranged from low to high magnitudes, in negative and positive directions. The estimates of genetic, phenotypic and environmental correlation of naupliar length and age at sexual dimorphism are presented in Table 27.

2.3.5 Naupliar length and length at first offspring laid

Although the naupliar length showed negative and weak correlation coefficients with length at first offspring laid in base and first generations of both the lines, the subsequent generations showed positive correlation with improved magnitude. The pooled genetic correlation coefficients were of high magnitude in BNS line (0.7934 ± 0.0107), but of moderate magnitude in SNS line (0.2519 ± 0.0348).

Phenotypic correlations were of lower magnitudes. The estimates were negative in base and first generation of SNS, whereas, in BNS line it was negative in third generation also. The estimates of the pooled correlation coefficients were 0.0302 ± 0.0463 and 0.0807 ± 0.0506 in SNS and BNS lines respectively. The environmental correlations were just the opposite of genetic and

Table 27 Genetic, phenotypic and environmental correlations between selected trait (naupliar length) and unselected trait (age at sexual dimorphism) in SNS and BNS lines.

Line	Generation	Male					Female				
		r_G	±S.E.	r_P	±S.E.	r_E	r_G	±S.E.	r_P	±S.E.	r_E
SNS	0	-0.5563	0.0409	-0.3215	0.0619	0.7483	-0.3490	0.0702	-0.1303	0.0626	0.4321
	1	0.0325	0.0569	0.0021	0.0676	-0.1111	0.0266	0.0445	-0.0027	0.0731	-0.1025
	2	-0.0395	0.1369	-0.0433	0.0645	-0.0294	-1.3353	0.2825	-0.2148	0.0592	-0.0606
	3	-0.0442	0.1036	-0.0005	0.0668	0.1610	0.0315	0.1144	-0.0263	0.0716	-0.2928
	4	0.2092	0.0789	0.1121	0.1014	-0.3173	0.0507	0.0989	0.0180	0.0814	-0.0834
	5	-0.0713	0.1422	0.0600	0.1052	0.5026	-0.1394	0.1035	-0.1551	0.0720	-0.6972
	6	-0.2531	0.0628	-0.1517	0.0926	0.3186	-0.5851	0.0625	-0.2432	0.0901	0.1487
Pooled		**-0.2312**	**0.0257**	**-0.0763**	**0.0283**	-	**-0.1836**	**0.0283**	**-0.1132**	**0.2682**	-
BNS	0	-0.5563	0.0409	-0.3215	0.0619	07483	-0.3490	0.0702	-0.1303	0.0626	0.4321
	1	0.0366	0.0925	-0.0160	0.0743	-0.1989	0.0023	0.0615	0.0067	0.0769	0.0151
	2	-0.0037	0.0763	-0.0050	0.0688	-0.0066	-0.2342	0.1526	0.0023	0.0743	0.2575
	3	-0.1097	0.1328	-0.0958	0.0789	0.0168	0.2353	0.0962	0.0342	0.0813	-0.5334
	4	0.5323	0.0570	0.2215	0.1259	-1.0644	0.4154	0.0378	0.2352	0.1042	-0.3928
	5	-0.1281	0.4392	-0.0186	0.1147	0.3965	0.8823	0.0117	0.4474	0.0694	-1.0268
Pooled		**-0.1368**	**0.0282**	**-0.0951**	**0.0324**	-	**0.7745**	**0.0108**	**0.0833**	**0.0308**	-

phenotypic correlations as far as direction was concerned. In base population and initial generations, the coefficients were positive, whereas, in the later generations they were negative. The estimates are presented in Table 28.

2.3.6 Naupliar length and age at first offspring laid

The genetic correlation coefficients in SNS line were of low to moderate magnitude and positive excepting first and fourth generations, in which the estimates were negative. In BNS, the r_G were positive and moderate to high in magnitude except the first generation, where it was negative and low. The pooled genetic correlation coefficients were 0.1469 ± 0.0269 and 0.9946± 0.003 in SNS and BNS lines respectively.

Phenotypic correlations were of low magnitude except the fourth and fifth generation of BNS line. They were negative in first and fourth generations in SNS and first generation in BNS, as in case of genetic correlation. The pooled r_P were 0.0729 ± 0.0458 and 0.2331 ± 0.0448 in SNS and BNS respectively. The environmental correlation coefficients were mostly negative except for first and fourth generation of SNS and second generation of BNS. The estimates of genetic, phenotypic and environmental correlation coefficients are presented in Table 29.

2.3.7 Naupliar length and number of offsprings in first brood

Genetic correlations were positive in base population, but showed negative correlation in the fifth generation of both the lines. The pooled genetic correlation coefficients were also negative, there values being -0.3347 ± 0.0350 and -0.4807 ± 0.0215 in SNS and BNS lines respectively.

Table 28 Genetic, phenotypic and environmental correlations between selected trait (naupliar length) and unselected trait (length at first offspring laid) in SNS and BNS lines.

Generations	SNS (Female)					BNS (Female)				
	r_G	±S.E.	r_P	±S.E.	r_E	r_G	±S.E.	r_P	±S.E.	r_E
0	-0.0689	0.0837	-0.0265	0.0808	0.0554	-0.0689	0.0837	-0.0265	0.0808	0.0554
1	-0.1352	0.1229	-0.0249	0.1020	0.2662	-0.07417	0.1481	-0.0326	0.1178	0.3538
2	0.3495	0.0549	0.0863	0.1265	-1.6087	0.3300	0.1663	-0.0104	0.1428	-0.3114
3	0.2576	0.0928	0.0600	0.1578	-0.3984	0.1466	0.0459	0.0524	0.2179	-0.2180
4	0.1656	0.1306	0.1160	0.1316	0.1101	0.5743	0.0489	0.2607	0.1734	-0.7767
5	0.6527	0.0961	0.1053	0.1317	-0.7029	0.8699	0.0115	0.4612	0.1268	-1.0263
Pooled	**0.2518**	**0.0348**	**0.03021**	**0.0463**	-	**0.7934**	**0.0107**	**0.0807**	**0.0506**	-

Table 29 Genetic, phenotypic and environmental correlations between selected trait (naupliar length) and unselected trait (age at first offspring laid) in SNS and BNS lines.

Generations	SNS (Female)					BNS (Female)				
	r_G	±S.E.	r_P	±S.E.	r_E	r_G	±S.E.	r_P	±S.E.	r_E
0	0.4969	0.0517	0.1906	0.0794	-1.0345	0.4969	0.0517	0.1906	0.0794	-1.0345
1	-0.1455	0.0559	-0.0779	0.1018	0.2326	-0.1342	0.057	-0.1617	0.1163	-0.0822
2	0.1884	0.0555	0.1108	0.1262	-0.3423	0.4424	0.0695	0.1564	0.1411	0.8149
3	0.4336	0.0795	0.1818	0.1515	-0.9393	0.4149	0.056	0.1971	0.2139	-0.4914
4	-0.3925	0.0734	-0.1632	0.1307	0.5072	0.7581	0.0251	0.4766	0.1579	-0.6406
5	0.3237	0.2107	0.1178	0.1315	-0.1364	0.9947	0.0003	0.6202	0.1121	-0.8210
Pooled	**0.1469**	**0.0269**	**0.0729**	**0.0458**	-	**0.9946**	**0.0003**	**0.2331**	**0.0448**	-

Phenotypic correlations showed almost the same trend as the genetic correlations, but were of low magnitude in both lines. The pooled phenotypic correlation coefficients were 0.0207 ± 0.0461 and - 0.0477 ± 0.0501 in SNS and BNS lines respectively. The environmental correlation coefficient were negative in base population but positive in fifth generation. Genetic, phenotypic and environmental correlation coefficients are presented in Table 30.

3.0 RESPONSE TO SELECTION

3.1 DIRECT RESPONSE TO SELECTION

Bi-directional individual selection was practised in two sub lines of *Artemia* to bring about change in the naupliar size. While the selection was for Small Naupliar Size in one line (SNS line) it was for Big Naupliar Size in the other (BNS line). The responses in each of these lines undergoing selection in diametrically opposite directions are presented below.

3.1.1 Selection differentials and selection intensities

Expected and effective selection differentials and ratios of expected to effective are presented, sex-wise, in Table 31 for SNS and BNS lines. It can be seen from the table that both expected and effective selection differentials were almost of the same magnitude in both the lines except in second generation of BNS line. Both expected and effective selection differentials averaged over generations were slightly higher in females of both SNS and BNS lines. The mean values for expected and effective selection differentials were -16.6780 μm and -16.3966 μm in SNS males, -19.9266 μm and -22.3101 μm in SNS females.

Table 30 Genetic, phenotypic and environmental correlations between selected trait (naupliar length) and unselected trait (Number of offsprings in first brood) in SNS and BNS lines.

Generations	SNS (Female)					BNS (Female)				
	r_G	±S.E.	r_P	±S.E.	r_E	r_G	±S.E.	r_P	±S.E.	r_E
0	0.2684	0.0828	0.1225	0.0802	-0.2684	0.2684	0.0828	0.1225	0.0802	-0.2684
1	-0.701	0.0813	-0.0358	0.102	0.1299	0.0578	0.1422	-0.1361	0.1168	-0.9578
2	0.0458	0.1232	0.0688	0.1267	1.2957	0.5757	0.0757	0.244	0.1385	-1.3921
3	0.2636	0.134	0.0025	0.1581	-5.2305	-0.1675	0.0608	-0.0995	0.2171	0.1597
4	-0.3548	0.1142	-0.1271	0.1314	0.6168	-0.5722	0.0879	-0.29	0.1719	3.1997
5	-0.6123	0.0557	-0.1966	0.1299	1.5939	-0.7631	0.0268	-0.463	0.1266	0.7068
Pooled	**-0.3347**	**0.0350**	**0.0207**	**0.0461**	-	**-0.4807**	**0.0215**	**-0.0477**	**0.0501**	-

Table 31 Expected and effective selection differentials of selected trait (Naupliar length).

Line	Parents of	Selection differential				Average (Sm + Sf)/2		Expected / Effective
		Male (Sm)		Female (Sf)				
		Expected	Effective	Expected	Effective	Expected	Effective	
SNS	S1	-22.3572	-22.6214	-29.0732	-34.6934	-25.7152	-28.6574	0.8973
	S2	-7.5564	-07.6271	-09.7647	-09.5395	-08.6606	-08.5833	1.0090
	S3	-22.5564	-19.9178	-20.9441	-23.6779	-21.7502	-21.7978	0.9978
	S4	-21.0624	-22.2104	-22.6878	-22.7640	-21.8751	-22.4872	0.9727
	S5	-11.4735	-10.5024	-14.6694	-16.0655	-13.0714	-13.2839	0.9840
	S6	-15.0626	-15.5006	-22.4208	-27.1208	-18.7417	-21.3107	0.8794
BNS	S1	24.3535	24.2932	16.5644	16.8711	20.4090	20.5822	0.9916
	S2	12.3317	06.6932	10.5133	05.7445	11.4225	06.1883	1.8458
	S3	14.9593	17.7644	18.5833	21.0320	16.7713	19.3982	0.8646
	S4	19.9610	19.6422	19.1587	17.0895	19.5599	18.3659	1.0650
	S5	09.6486	10.9570	20.7704	23.9843	15.2095	17.4707	0.8706

The corresponding values in BNS line were 16.2308 μm and 15.8700 μm for males and 17.1180 μm and 17.0019 μm for BNS females. The phenotypic standard deviations and intensity of selection are presented in Table 32.

3.1.2 Phenotypic response

The generation-wise mean values of naupliar length of both SNS and BNS lines are presented, sex-wise, in Table 33. The mean naupliar length of SNS in males and females were 441.6735 ± 2.3345 μm and 453.0534 ± 3.6845 μm respectively, after six generation of individual selection, as against 486.9912 ± 2.1136 μm and 490.5754 ± 1.8157 μm in the base generation. The corresponding mean values in BNS were 495.5835 ± 2.8021 μm and 529.3720 ± 2.7009 μm in fifth generation as against 486.9912 ± 2.1136 μm and 490.5754 ± 1.8157 μm in the base generation.

The mean naupliar length of females were always more than those of males in both of the selected line as well as in control line, though the differences were not statistically significant except in the first, third and sixth generation of SNS and base, fourth and fifth generation of BNS line.

The total phenotypic response i.e. cumulative decrease in naupliar size, from six generations of selection for small naupliar size was - 45.3177 μm in males and - 37.5220 μm in females of SNS line. The corresponding values in BNS line were 8.5923 μm and 38.7966 μm for males and females respectively. In the SNS line the average phenotypic response calculated from regression of generation means on generation numbers were - 5.7554 ± 1.4947 μm and - 4.9743 ±1.1997 μm in male and females of respectively. The corresponding

Table 32 Phenotypic standard deviation and selection intensities of selected trait (Naupliar length) in individual selection.

Line	Parents	Phenotypic Standard deviation (σ_P)		Selection intensity		Average (im+if) / 2
		Male	Female	Male	Female	
SNS	S1	32.6751	29.0519	-0.6923	-1.1942	-0.9433
	S2	23.9953	25.1242	-0.3179	-0.3797	-0.3487
	S3	24.9532	24.5385	-0.7982	-0.9649	-0.8816
	S4	27.7239	31.5053	-0.8011	-0.7225	-0.7618
	S5	21.3425	22.5058	-0.4921	-0.7138	-0.6030
	S6	29.4958	27.7016	-0.5255	-0.9790	-0.7523
Average		**26.6976**	**26.7379**	**-0.6045**	**-0.8257**	**-0.7151**
BNS	S1	32.6751	29.0519	0.7435	0.5807	0.6621
	S2	26.9532	26.5514	0.2461	0.2164	0.2312
	S3	23.6426	27.3393	0.7513	0.7687	0.7600
	S4	28.5118	30.9818	0.6889	0.5516	0.6203
	S5	26.1223	32.0504	0.4195	0.7483	0.5839
Average		**27.5810**	**29.1950**	**0.5699**	**0.5731**	**0.5715**

Table 33. Mean, standard error and coefficient of variation of (%) naupliar length in SNS and BNS lines.

Line	Generation	Male			Female		
		N	$\overline{X}$ µm ±S.E.	C.V (%)	N	$\overline{X}$ µm ±S.E.	C.V (%)
SNS	0	239	486.9912 ±2.1136	6.71	255	490.5754 ±1.8157	5.92
	1	223	467.5543 ±1.6068	5.13	195	472.8036 ±1.7946 ++	5.31
	2	246	467.8579 ±1.5877	5.33	275	471.2891 ±1.4797	5.21
	3	226	453.1580 ±1.8442	6.12	202	459.7709 ±2.2112 ++	6.85
	4	102	466.6716 ±2.1132	4.57	154	469.4052 ±1.8077	4.79
	5	095	455.5490 ±3.0104	6.47	190	460.3879 ±2.0097	6.02
	6	116	441.6735 ±2.3345	5.72	118	453.0534 ±3.6845 ++	8.83
	b±S. E. @	-	**-5.7554 ±1.4947 ****	-	-	**-4.9743 ±1.1997 ***	-
BNS	0	239	486.9912 ±2.1136	6.71	255	490.5754 ±1.8157 +	5.92
	1	187	504.5246 ±1.9710	5.34	171	506.1070 ±2.0245	5.25
	2	216	491.7750 ±1.6087	4.81	186	494.7871 ±2.006	5.53
	3	163	492.7043 ±2.2332	5.79	153	496.2098 ±2.5047	6.24
	4	065	494.4246 ±3.2401	5.28	091	505.3978 ±3.3415 ++	6.34
	5	079	495.5835±2.8021	5.03	168	529.3720 ±2.7009 ++	6.61
	6	-	-	-	-	-	-
	b± S. E. @	-	**0.3883 ±1.5395**	-	-	**5.5222 ±2.1979 ***	-

+ and ++ indicates that female naupliar length is significantly different from male naupliar length at $P< 0.05$ and $P< 0.01$ respectively.
* and ** indicates that 'b' values are significant at $P<0.05$ and $P< 0.01$ respectively.
@ regression of generation means on generation number

Fig. 2 Linear trend of phenotypic response in naupliar length of SNS males

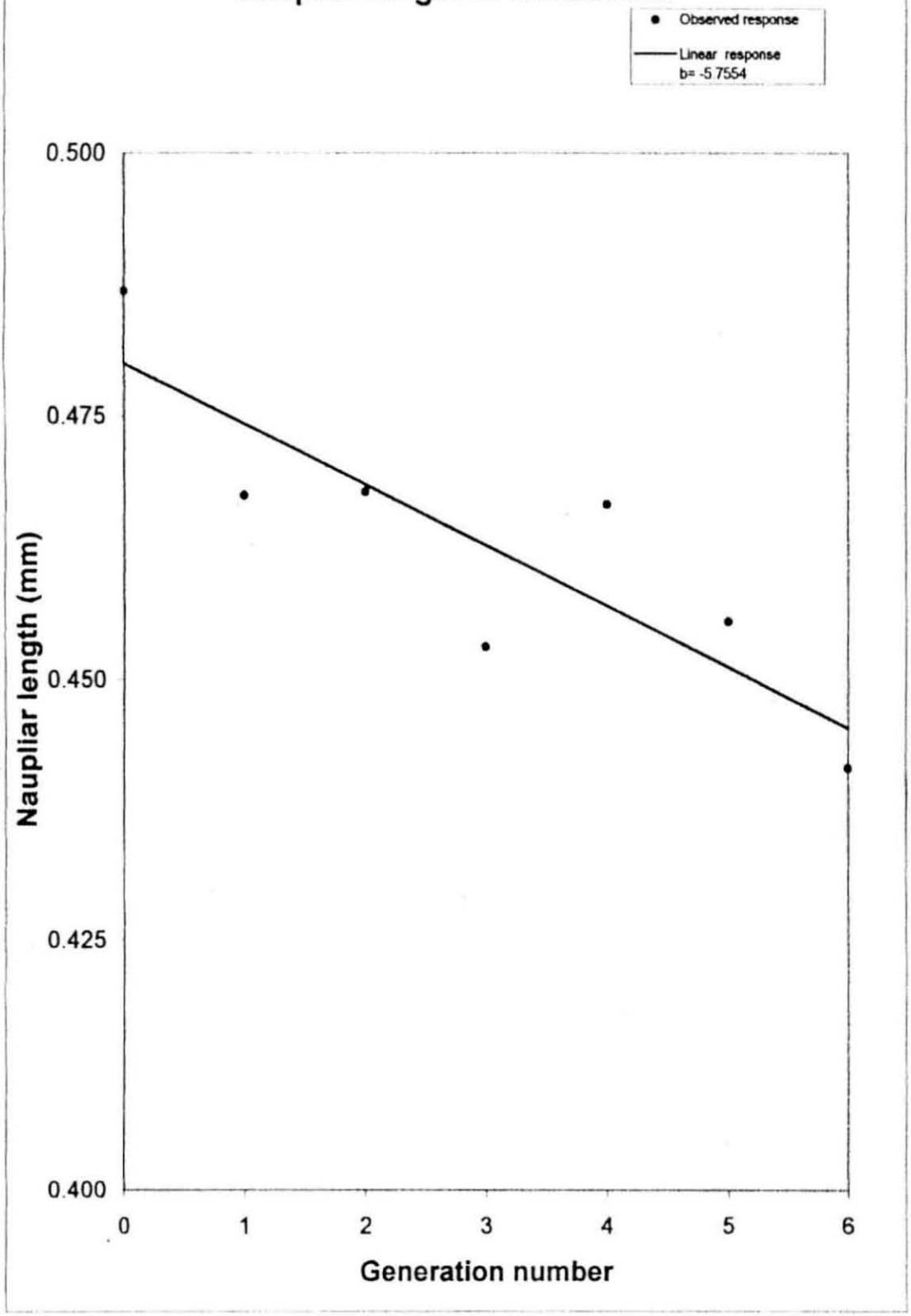


Fig. 3 Linear trend of phenotypic response in naupliar length of SNS females

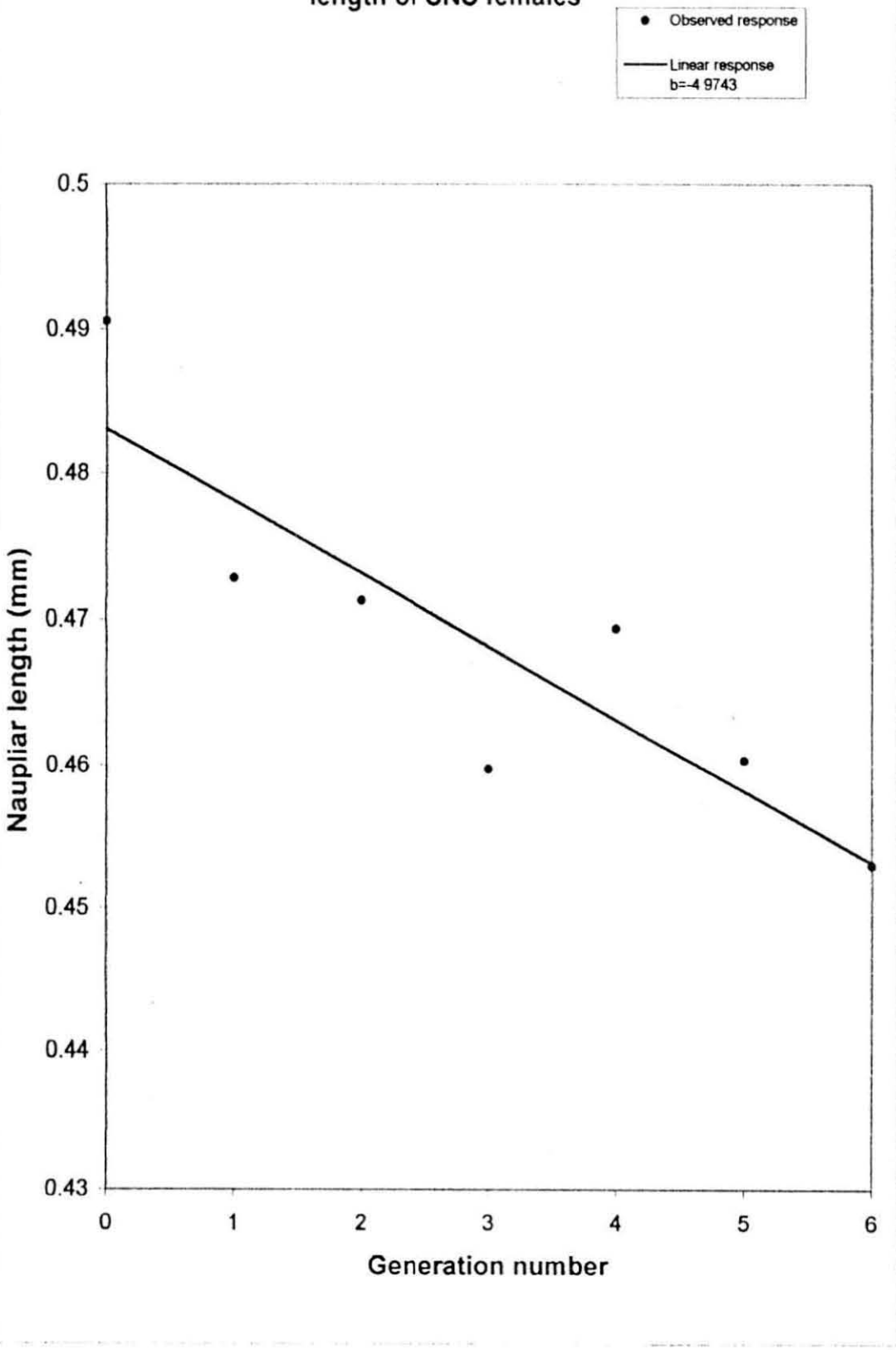


Fig. 4 Linear trend of phenotypic response in naupliar length of BNS males

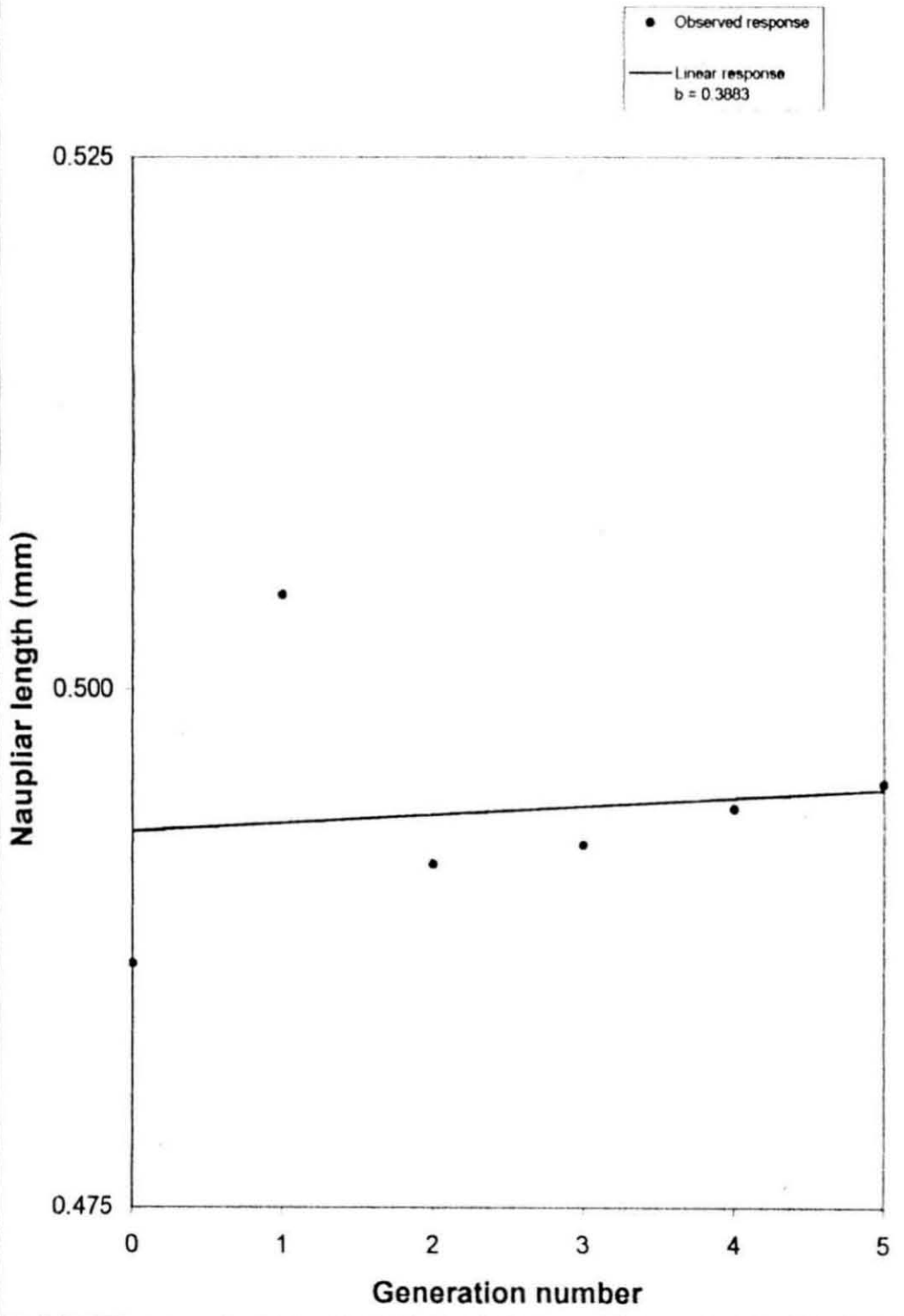
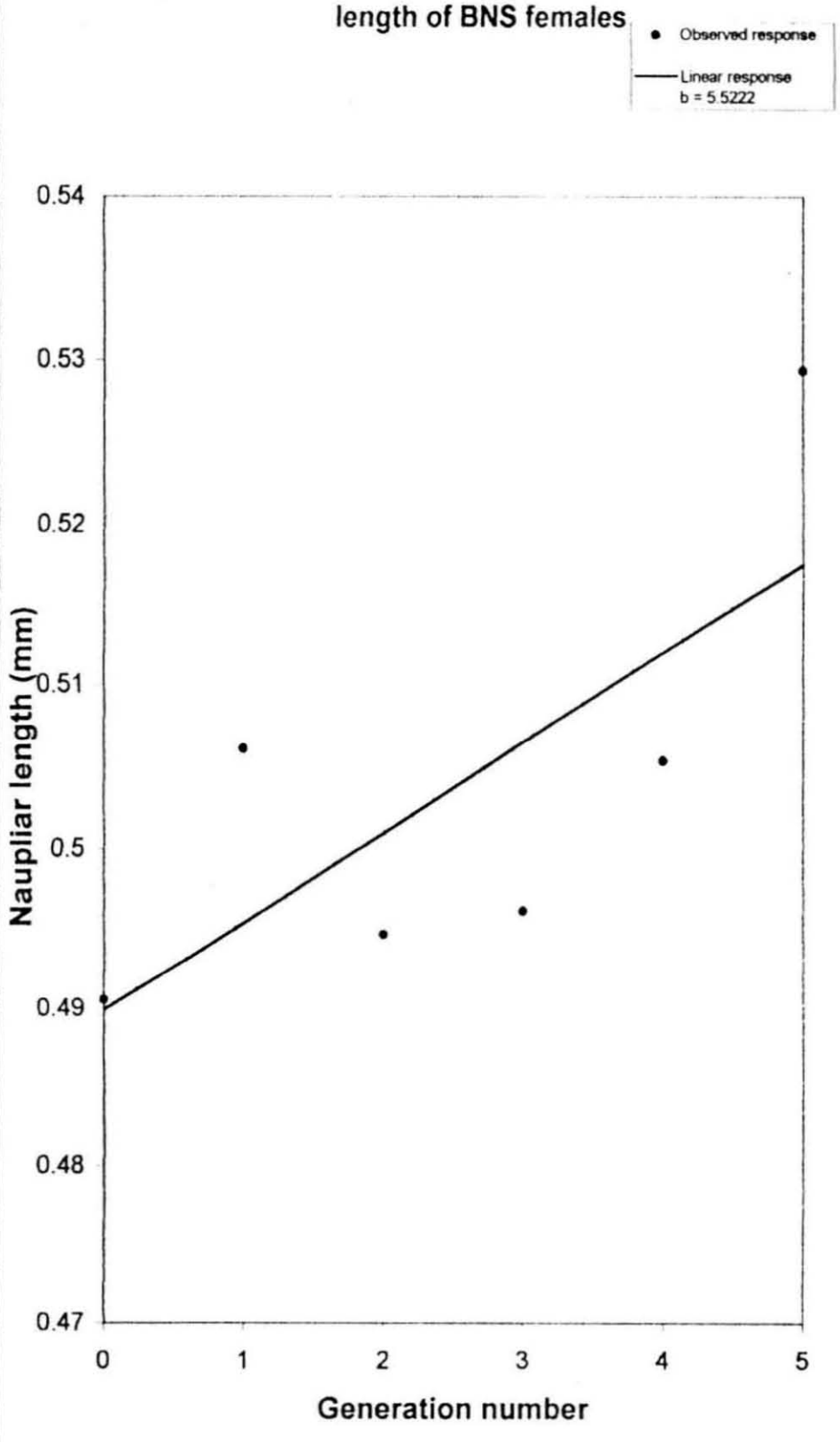


Fig. 5 Linear trend of phenotypic response in naupliar length of BNS females



values in BNS line were 0.3883 ± 1.5395 μm and 5.5222 ± 2.1979 μm. The mean phenotypic responses were statistically significant except that of BNS males.

3.1.3 Realized genetic gain

The observed phenotypic response is the combined effect of both genetic and environmental factors. Since the environment rarely remains same over the period of selection, separating out these effects becomes rather difficult. One of the most common methods for measuring environmental trend is the use of an unselected control population, preferably from the same stock, as that of a selected population. Such a control line was used in the present study also.

The mean naupliar length of control line used in the study is presented sex-wise and generation-wise in Table 34. Though the mean naupliar length varied from generation to generation, the regression of control mean on the generation number was non-significant. This fact suggests that, the fluctuations in the control mean were due to random changes in the environment. Consequently, the genetic gains in the selected generations were calculated after correction of generation mean of the selected lines to control means. The cumulative genetic gains realized in each generation of the two lines, estimated as control deviations, are presented in Table 35 and Fig. 6 to 9.

In the SNS line, the total genetic gains, i.e. decrease in naupliar length realized from six generations of individual selection for smaller naupliar length, was - 41.7244 μm in males and - 38.7585 μm in females. However, in BNS line, the total genetic gains from five generations of selection were 12.6427 μm and 39.4836 μm in males and females respectively.

Table 34 Mean, standard error and coefficient of variation (%) of naupliar length in Control line.

Generation	Male			Female		
	N	$\bar{X}$ µm ±S.E.	C.V(%)	N	$\bar{X}$ µm ±S.E.	C.V(%)
0	239	486.9912 ±2.1136	6.71	256	490.5754 ±1.8157	5.92
1	098	486.6831 ±1.3985	2.85	112	490.9359±1.6230	5.34
2	075	483.3373 ±1.8828	3.37	091	489.0627±2.1917	4.81
3	070	481.474 ±2.0243	3.52	088	487.6298 ±2.3564	5.79
4	051	487.6906 ±2.2644	3.32	059	494.5766 ±2.6360	5.28
5	063	482.9408 ±2.2847	3.75	081	489.8884 ±2.6595	5.03
6	045	483.3979 ±2.7669	3.84	058	491.8119 ±3.2209	4.96
b±S. E.	-	**-0.4968 ±0.4492 NS**	-	**b ±S. E.**	**0.3883 ±1.5395 NS**	-

NS indicates not significant

Table 35 Cumulative genetic gain in naupliar length of SNS and BNS lines.

Sex	Generation	SNS			BNS		
		Selected (S)	Control (C)	Genetic gain (Sn-Cn)	Selected (S)	Control (C)	Genetic gain (Sn-Cn)
Male	0	486.9912	486.9912	0.0000	486.9912	486.9912	0.0000
	1	467.5543	486.6831	-19.1285	504.5246	486.6831	17.8415
	2	467.8579	483.3373	-15.4794	491.7750	483.3373	8.4377
	3	453.1580	481.474	-28.3160	492.7043	481.474	11.2303
	4	466.6716	487.6906	-21.0190	494.4246	487.6906	6.7340
	5	455.5490	482.9408	-27.3918	495.5835	482.9408	12.6427
	6	441.6735	483.3979	-41.7244	-	-	-
b±S. E.				**-5.2585 ±1.2517****			**0.9338 ±1.5409 NS**
Female	0	490.5754	490.5754	0.0000	490.5754	490.5754	0.0000
	1	472.8036	490.9359	-18.1323	506.1070	490.9359	15.1711
	2	471.2891	489.0627	-17.7736	494.7871	489.0627	5.7244
	3	459.7709	487.6298	-27.8589	496.2098	487.6298	8.5800
	4	469.4052	494.5766	-25.1714	505.3978	494.5766	10.8212
	5	460.3879	489.8884	-29.5005	529.3720	489.8884	39.4836
	6	453.0534	491.8119	-38.7585	-	-	-
b± S. E.		-	-	**-5.2289 ±0.9683 ****	-	-	**5.3493 ±2.5384 ***

* and ** indicates that 'b' values are significant at P<0.05 and P< 0.01 respectively.
NS indicates not significant.

Fig. 6 Linear trend of genetic gain in naupliar length of SNS males

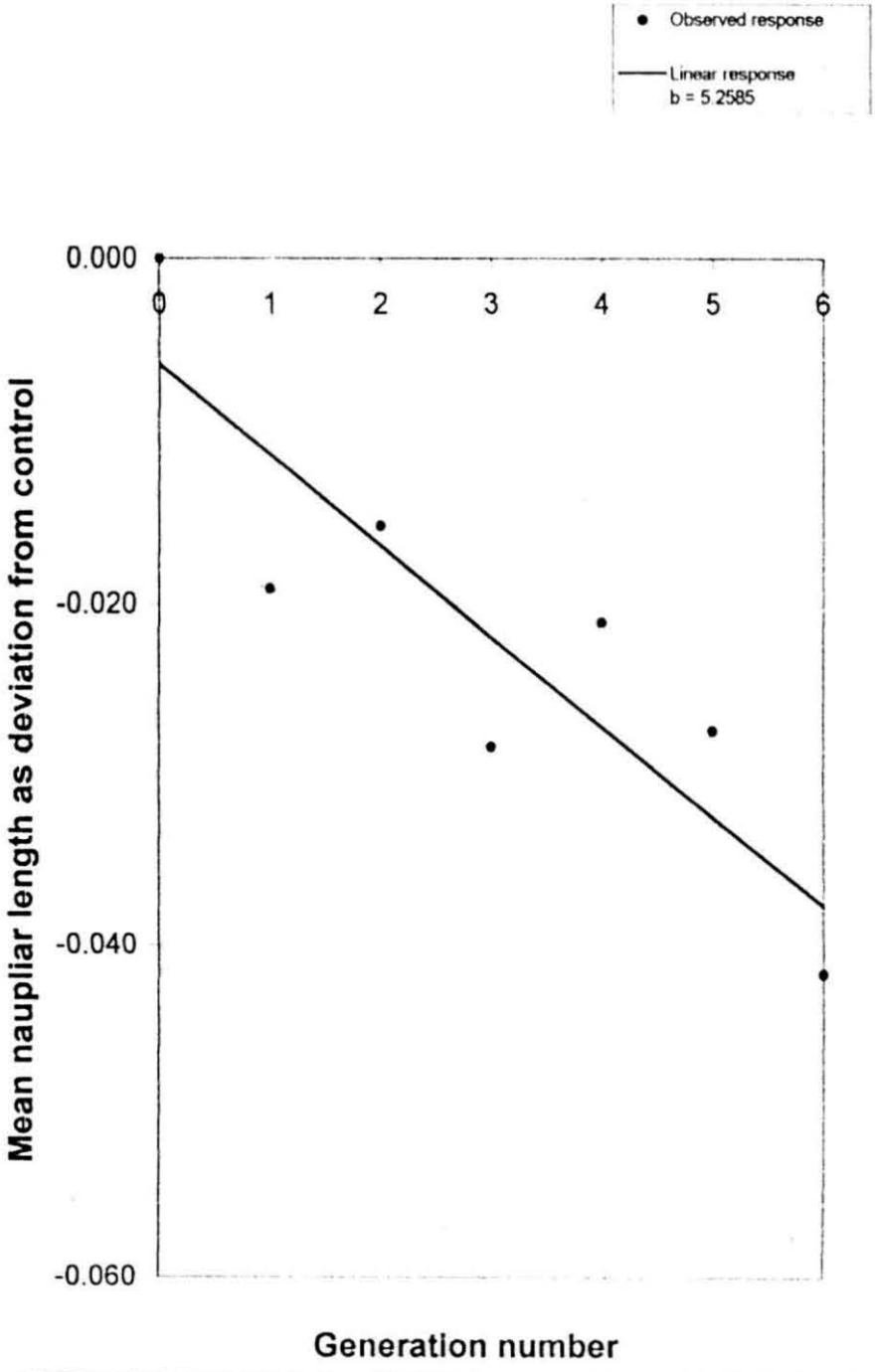


Fig. 7 Linear trend of genetic gain in naupliar length of SNS females

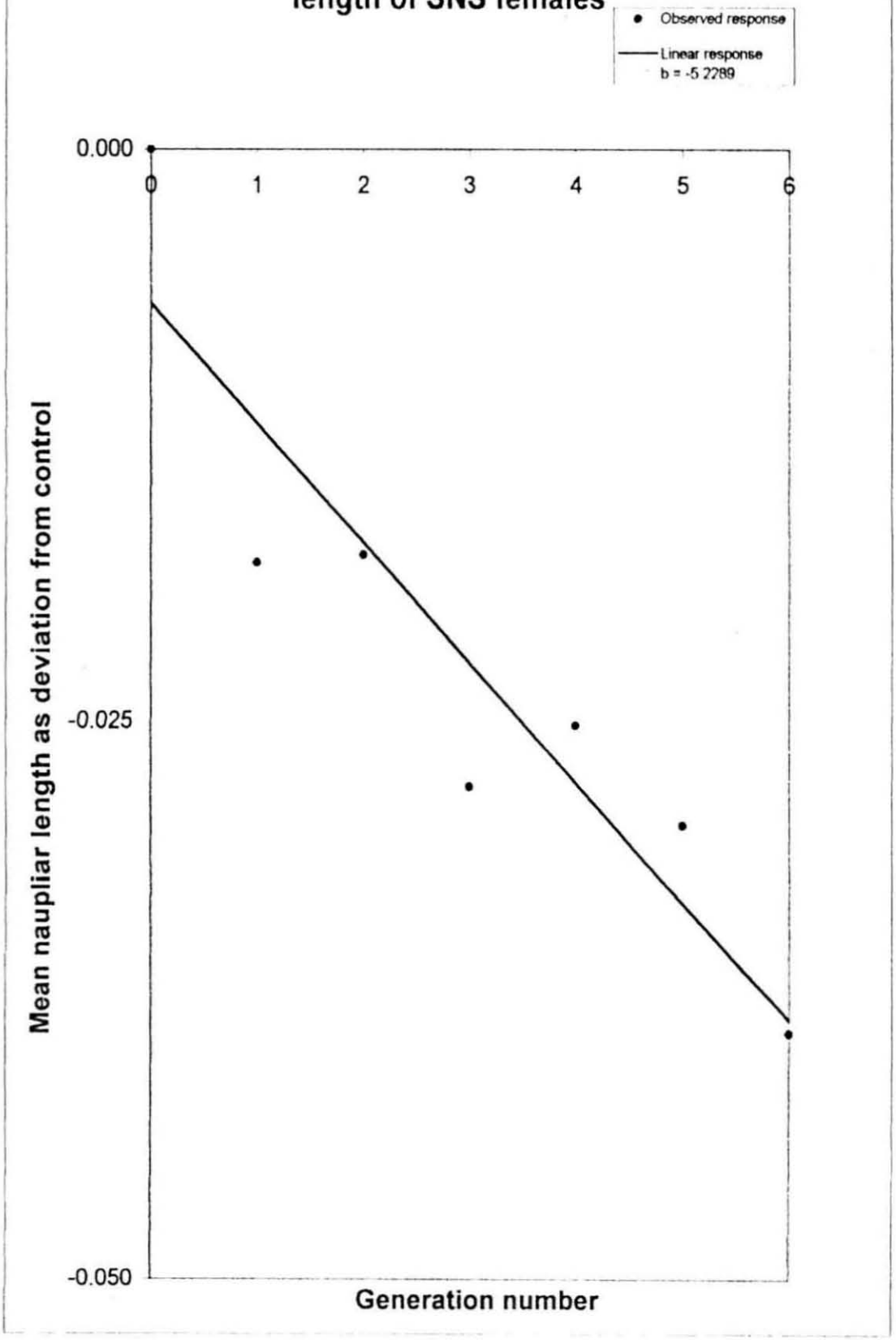


Fig 8 Linear trend of genetic gain in naupliar length of BNS males

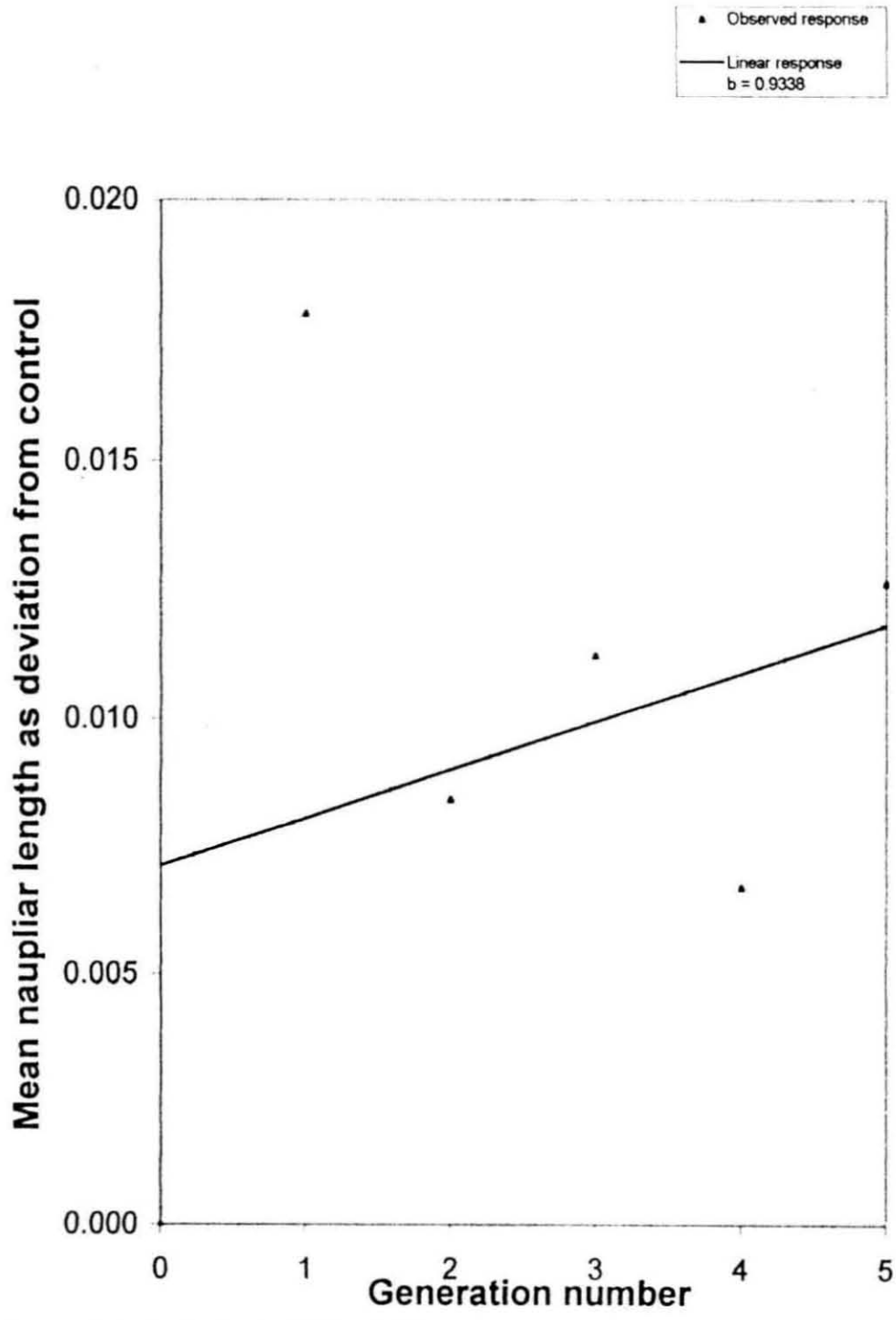
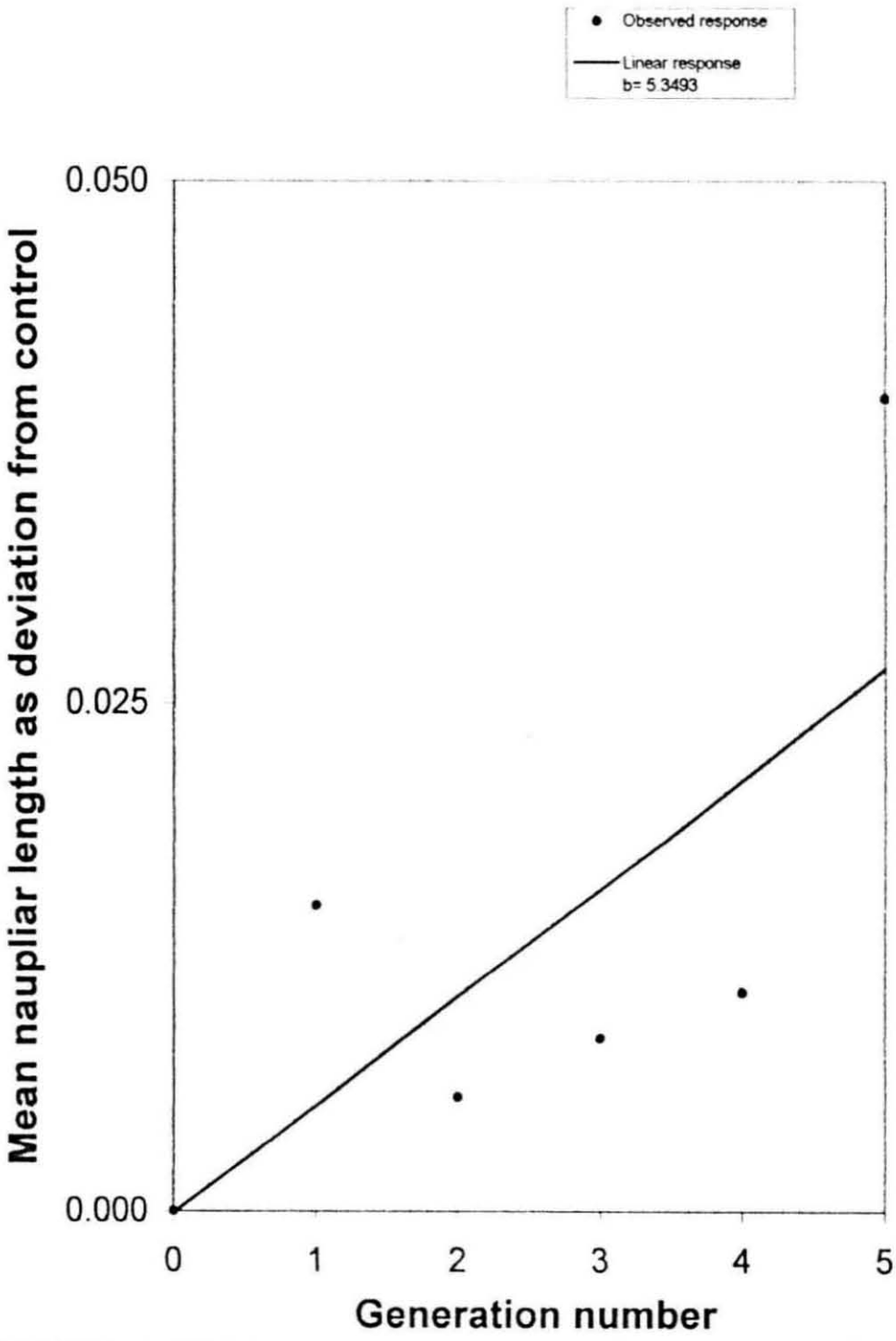


Fig 9 Linear trend of genetic gain in naupliar length of BNS females



The realized mean genetic gain per generation, estimated from the regression of control corrected generation means on generation numbers, were - 5.2585 ± 1.2517 µm in males and -5.2289 ± 0.9683µm females of SNS, and 0.9338 ± 0.9338 µm in males and 5.3493 ± 2.5384 µm in females of BNS line. The mean genetic gains were statistically significant except that of BNS males.

3.1.4 Predicted genetic gain

The expected mean genetic gain from six generations of individual selection for naupliar length in SNS and BNS lines were estimated separately for both sexes, using pooled estimates of heritability, mean phenotypic deviations of naupliar length from the generations from which parents were selected and selection intensities averaged over the generations. Two sets of predictions were made (1) by using pooled heritability estimates from full sib analysis and (2) by using heritability estimates from b_{op}. Values of both the predictions are presented in Table 36 along with realized mean genetic gain. The predicted mean genetic gains were compared with realized genetic gains. It can be seen from the table that prediction made with full sib heritability were much higher than realized gains, whereas the predictions made with b_{op} were more or less comparable to the realized gains. The ratios of the realized gains to the expected gains, which gives an indication of the effect of natural selection on artificial selection are also presented in Table 37. The ratio was highest in SNS male (1.5348) followed by BNS female (0.9503), SNS female (0.6096) and least in BNS male (0.1028) for b_{op} predictions.

Table 36 Predicted and realized mean genetic gain in naupliar size (selected trait) of SNS and BNS lines.

Line	Sex	Genetic gain			Ratio of realized gain to predicted gain from full sibs h^2	Ratio of realized gain to predicted gain from b_{op}
		Predicted using heritability estimates		Realized		
		Full sib	b_{op}			
SNS	Male	-21.3934	-3.4263	-5.2585	0.2302	1.5348
	Female	-24.2940	-8.5773	-5.2289	0.2152	0.6096
	Mean	-22.8437	-6.0018	-5.2437	0.2296	0.8737
BNS	Male	19.7738	9.0805	0.9338	0.0472	0.1028
	Female	23.7973	5.6292	5.3493	0.2248	0.9503
	Mean	21.7855	7.3591	3.1416	0.1442	0.4269

3.1.5 Time Trends in Phenotypic standard deviation

Time trends in phenotypic standard deviation (σ_P) of the naupliar length in the individual generations of SNS and BNS lines are presented sex-wise, in Table 37. The phenotypic standard deviation showed a declining trend (i.e. negative regression coefficient) in males of both SNS and BNS lines, but increasing trend (i.e. positive regression coefficient) in females, as the generations of selection advanced. The regression coefficients in males were -0.5315 ±0.7441 μm and -1.0421 ±0.6030 μm in SNS and BNS lines respectively. Corresponding values in females were 1.2871 ±1.0667 μm and 1.4256 ±0.4039 μm respectively. However, none of these regression coefficients were statistically significant.

3.1.6 Realized heritability

Realized heritabilities estimated for each of the six selected generations of SNS and five generations of the BNS are given in Table 38. The values were found to be moderately high, except a few, which were negative. The mean realized heritabilities in males and females were 0.4550 and 0.3056 in SNS line, and -0.0085 and 0.3143 in BNS line.

3.2 CORRELATED RESPONSE

3.2.1 Realized correlated response

Correlated phenotypic response in unselected traits like lengths on 3 days of age, length on 6 days of age, length at sexual dimorphism, age at sexual dimorphism, age at first offspring laid, length at first offspring laid and number of offsprings in first brood were estimated during the present study. Generation-

Table 37 Estimates of phenotypic standard deviation of naupliar size in SNS and BNS lines.

Generation	Phenotypic standard deviation					
	SNS		BNS		Control	
	Male	Female	Male	Female	Male	Female
0	32.6751	29.0519	32.6751	29.0519	32.6771	29.0519
1	23.9953	25.1242	26.9532	26.5514	13.8705	26.2160
2	24.9532	24.5385	23.6426	27.3593	16.2885	23.5239
3	27.7239	31.5053	28.5118	30.9818	16.9479	28.2338
4	21.3425	22.5058	26.1223	32.0504	16.1913	26.1136
5	29.4958	27.7016	24.9054	35.0074	18.1103	24.6414
6	25.2512	40.0241	-	-	18.5625	24.5414
b ± S. E.	**-0.5315 ±0.7441 NS**	**1.2871±1.0667 NS**	**-1.0421 ±0.6030 NS**	**1.4256 ±0.4039 NS**	**-3.2801 ±2.0273**	**-0.9174 ±0.5136**

NS indicates not significant.

Table 38 Realized heritability estimates of naupliar length in SNS and BNS lines.

Generation	Realized heritability			
	SNS		**BNS**	
	Male	Female	Male	Female
1	0.8694	0.6113	0.7229	0.9376
2	-0.0402	0.1551	-1.0339	-1.0767
3	0.6517	0.5500	0.0621	0.0766
4	-0.6416	-0.4246	0.0862	0.4796
5	0.9694	0.6147	0.1201	1.1543
6	0.9212	0.3271	-	-
Average	**0.4550**	**0.3056**	**-0.0085**	**0.3143**

wise estimates of mean values along with standard deviation, heritability as well as genetic and phenotypic correlation among the above traits are presented below.

3.2.1.1 Length on 3 days of age

The mean length on 3 days age in both SNS and BNS lines, along with the correlated response, are presented in Table 39, sex-wise, for each generation. Linear trend of correlated response in 3 day length of males and females of both the sexes are depicted in Fig 10 to 13. The direction of change in this unselected trait was same as that in the selected trait, over the generations i.e. a decrease in SNS line, and an increase in BNS line. While the 3rd day length of male decreased from 1.8679 mm of the base generation to 1.7067 mm in the sixth generation, increase in BNS line was from 1.8679 mm to 2.2967 mm. Correspondingly, in females, the length on 3 days of age decreased from 1.8712 ± 0.0270 to 1.7363 ± 0.3066 mm in SNS line and increased from 1.8712 ± 0.0270 to 1.9512 ± 0.3010 mm in BNS line. The regression coefficient of generation means on generation numbers in males and females of SNS line were -0.0257 ± 0.0136 mm and -0.0333 ± 0.0185 mm respectively. The corresponding values in BNS line were 0.0369 ± 0.0377 mm and -0.0087 ± 0.0211 mm. However, none of these values were found to be statistically significant.

The generation means were tested for the significance of difference from base population mean, and most of them were found to be significantly different (Table 39).

3.2.1.2 Length on 6 days of age

The mean values of length on 6th day, along with standard errors and correlated response are presented in Table 40. Unlike the length on 3rd day,

Table 39 Mean ($\overline{X}$), Standard deviation (SE) and correlated response of length on 3rd day in SNS and BNS lines.

Line	Generation	Male		Female	
		$\overline{X}$ (mm) ± SE	Correlated response	$\overline{X}$ (mm)±SE	Correlated response
SNS	0	1.8679 ±0.0275	0.0000	1.8712 ±0.0270	0.0000
	1	1.8031 ±0.0199	-0.0648	1.8485 ±0.0218	-0.0227
	2	1.9474 ±0.0217*	0.0795	1.9310 ±0.0213	0.0598
	3	1.7167 ±0.0200**	-0.1512	1.7563 ±0.0224**	-0.1149
	4	1.7521 ±0.0313*	-0.1158	1.5791 ±0.0275**	-0.2921
	5	1.7825 ±0.0335	-0.0854	1.7600 ±0.0235**	-0.1112
	6	1.7067 ±0.0279**	-0.1612	1.7363 ±0.3066**	-0.1349
b±S. E.	-	**-0.025 7± 0.0136 NS**	-	**-0.0333 ± 0.0185 NS**	-
BNS	0	1.8679 ±0.0275	0.0000	1.8712 ±0.0270	0.0000
	1	2.0690 ±0.0277**	0.2011	2.0196 ±0.0299**	0.1484
	2	2.0576 ±0.0312**	0.1897	2.0229 ±0.0289**	0.1517
	3	1.9751 ±0.0291**	0.1072	1.9844 ±0.0302**	0.1132
	4	1.8123 ±0.0456	-0.0556	1.7972 ±0.0353	-0.0740
	5	2.2967 ±0.0526**	0.4288	1.9512 ±0.0310	0.0800
b±S. E.	-	**0.0369 ± 0.0377 NS**	-	**-0.0087 ± 0.0211 NS**	-

* and ** indicate the significance difference from base population at P<0.05 and P<0.01 respectively.
NS – Non-significant

Fig. 10 Linear trend of correlated response in 3-day length of SNS males

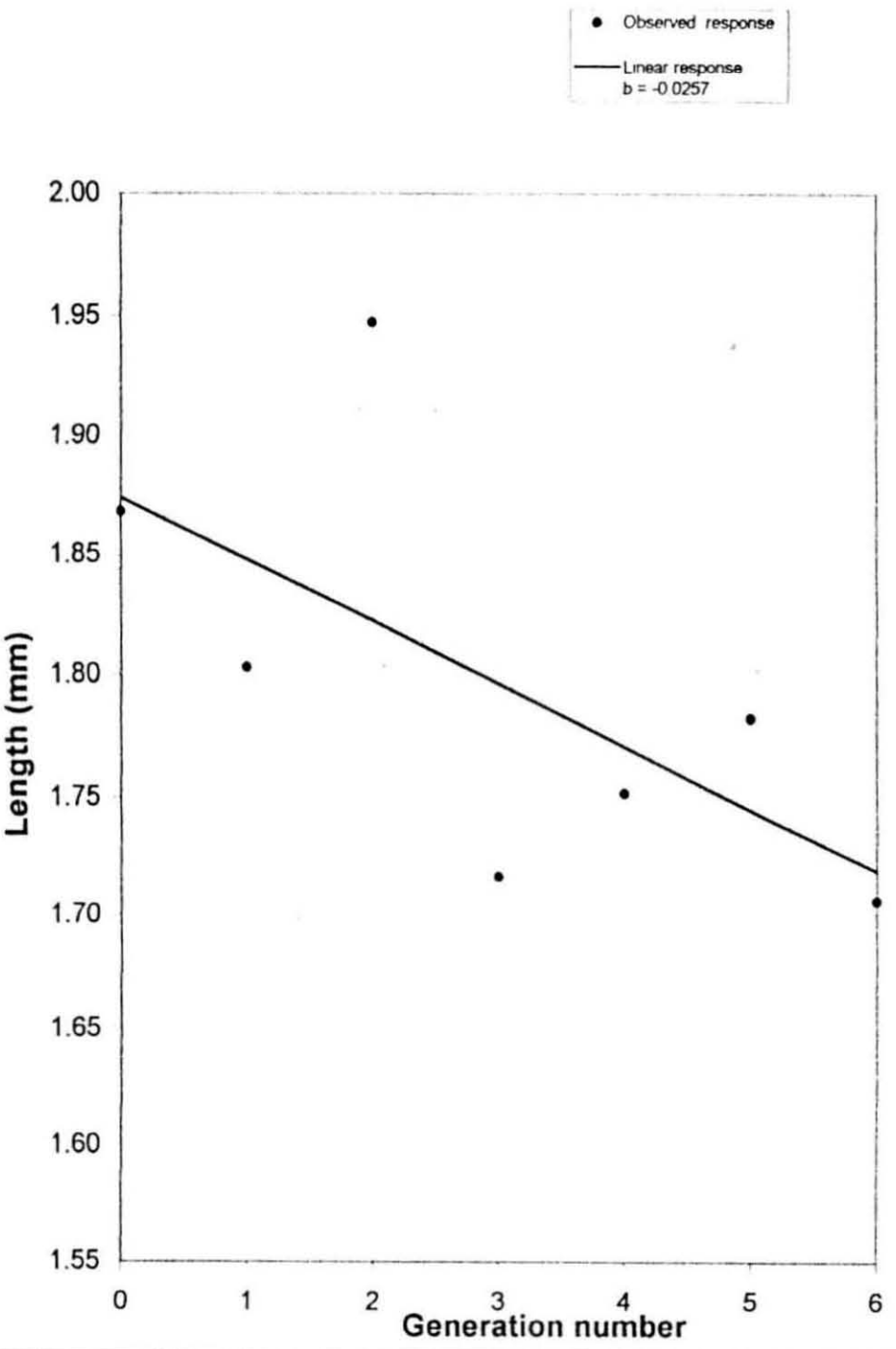


Fig. 11 Linear trend of correlated response in 3-day length of SNS females

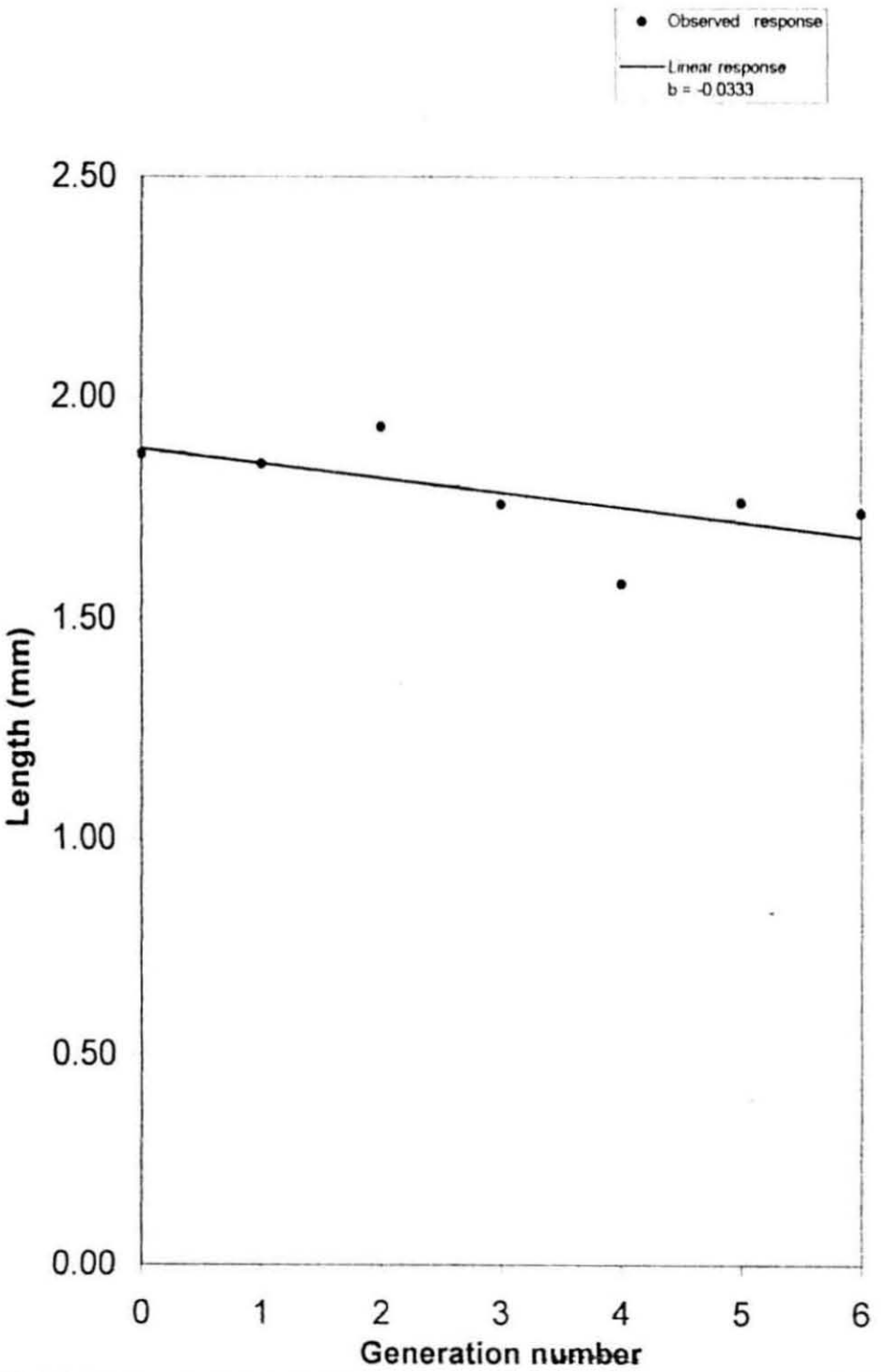


Fig. 12 Linear trend of correlated response in 3-day length of BNS males

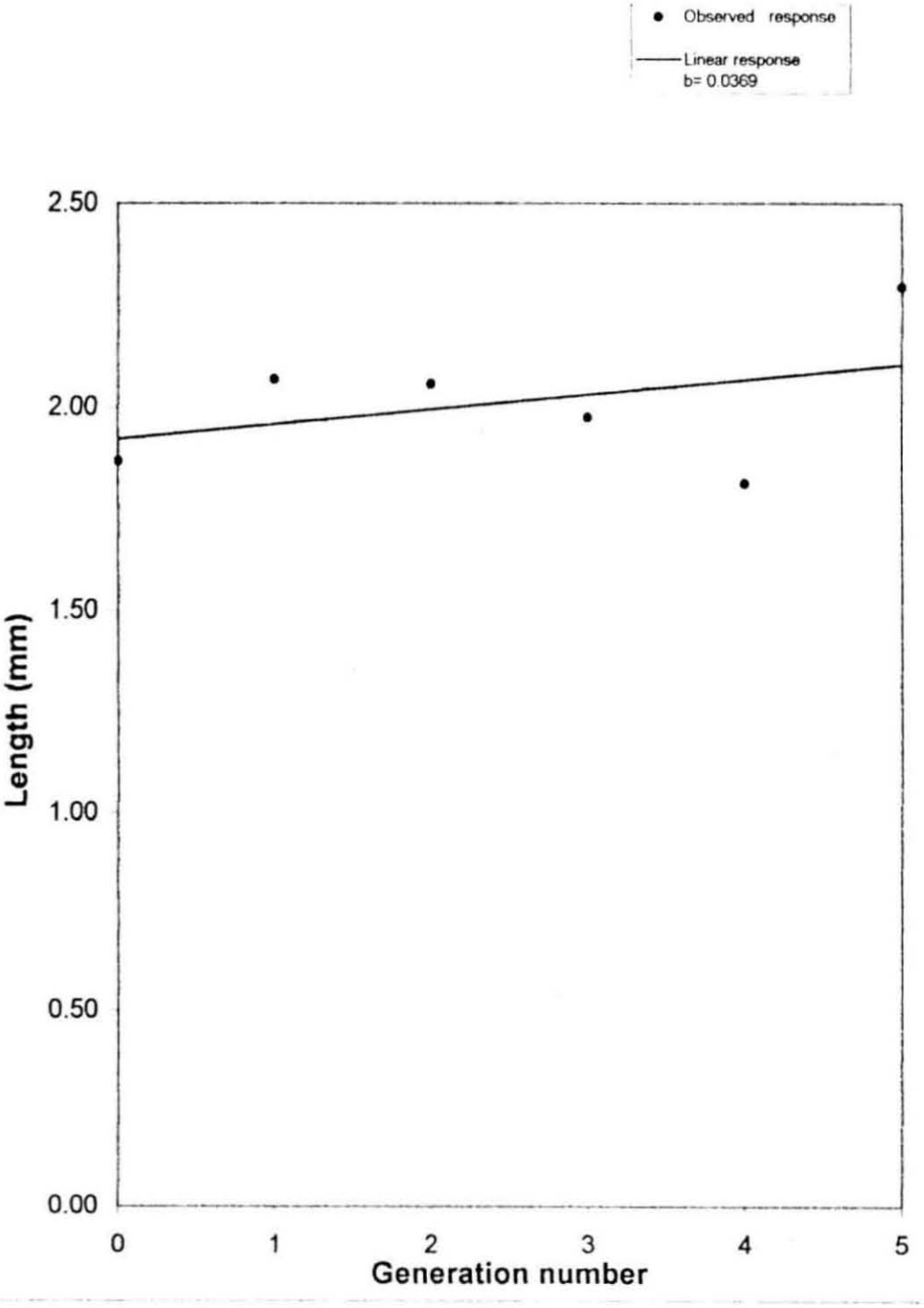


Fig. 13 Linear trend of correlated response in 3-day length of BNS females

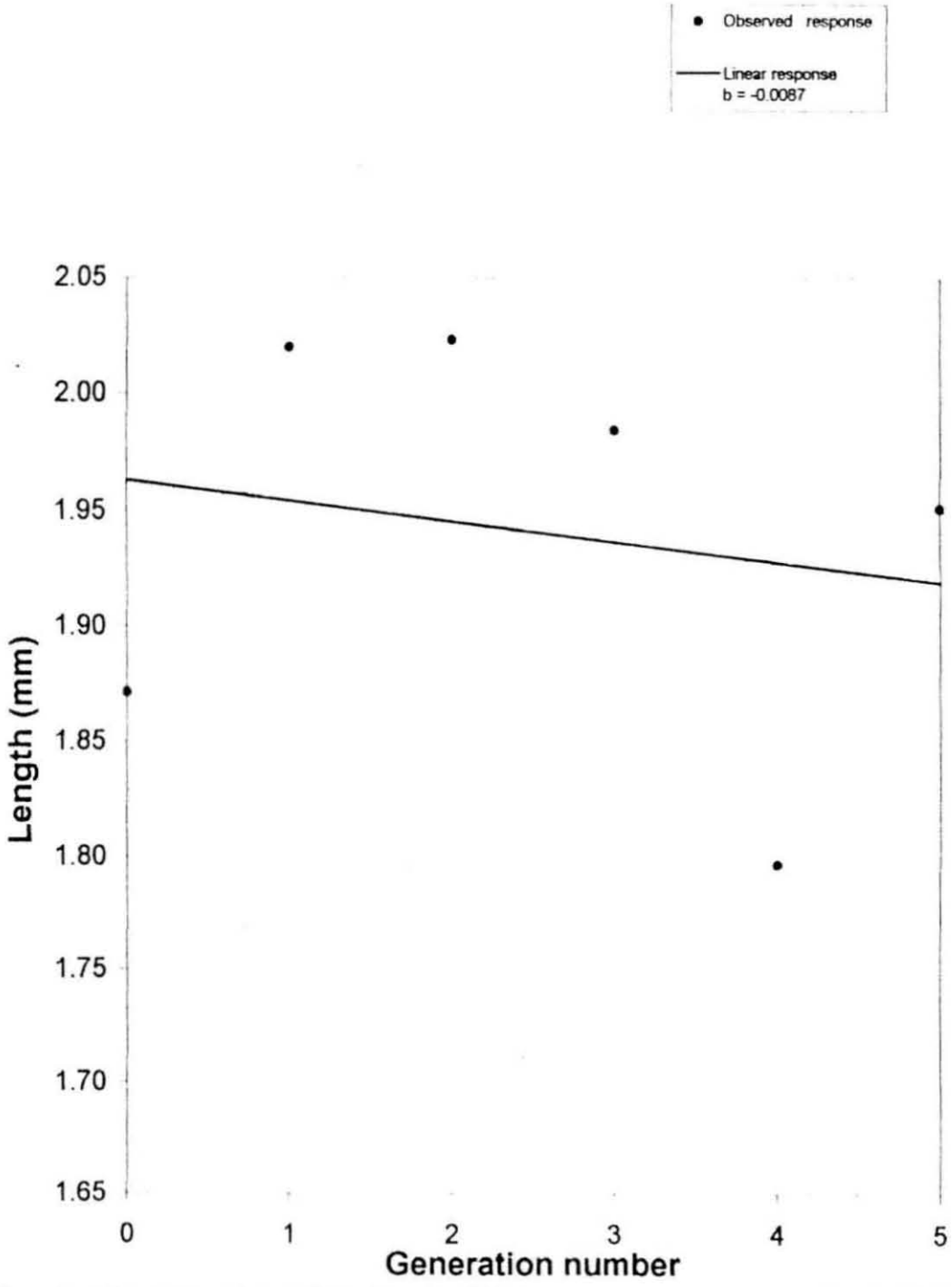


Table 40 Mean ($\overline{X}$), Standard deviation (S.E.) and correlated response of length on 6th day in SNS and BNS lines.

Line	Generation	Male		Female	
		$\overline{X}$ (mm)±SE	Correlated response	$\overline{X}$ (mm)±SE	Correlated response
SNS	0	4.1005 ±0.0754	0.0000	4.2990 ±0.0793	0.0000
	1	5.0955 ±0.0737**	0.995	5.5144±0.0970**	1.2154
	2	5.5441 ±0.0567**	1.4436	6.0282 ±0.0690**	1.7292
	3	4.6867 ±0.0583**	0.5862	4.9680 ±0.0614**	0.6690
	4	4.5637 ±0.1365**	0.4632	4.0162 ±0.1274**	-0.2828
	5	4.6718 ±0.1003**	0.5713	4.6310 ±0.0855**	0.3320
	6	4.1980 ±0.1046	0.0975	4.5868 ±0.1187	0.2878
b±S. E.		**-0.0548 ±0.1006 NS**	-	**-0.1041 ±0.1377 NS**	-
BNS	0	4.1005 ±0.0754	0.0000	4.2990 ±0.0793	0.0000
	1	5.3833 ±0.0838**	1.2828	5.7093 ±0.1002**	1.4103
	2	5.9710 ±0.0605**	1.8705	6.4144 ±0.0779**	2.1154
	3	5.0649 ±0.0716**	0.9644	5.4250 ±0.0784**	1.1260
	4	4.5008 ±0.1522**	0.4003	4.1834 ±0.1463	-0.1156
	5	5.7481 ±0.1142**	1.6476	4.8370 ±0.0884**	0.5380
b±S. E.	-	**0.1338 ±0.1621 NS**	-	**-0.0822 ±0.2036 NS**	-

* and ** indicate the significance difference from base population at $P<0.05$ and $P<0.01$ respectively.
NS indicates Not significant

Fig. 14 Linear trend of correlated response in 6-day length of SNS males

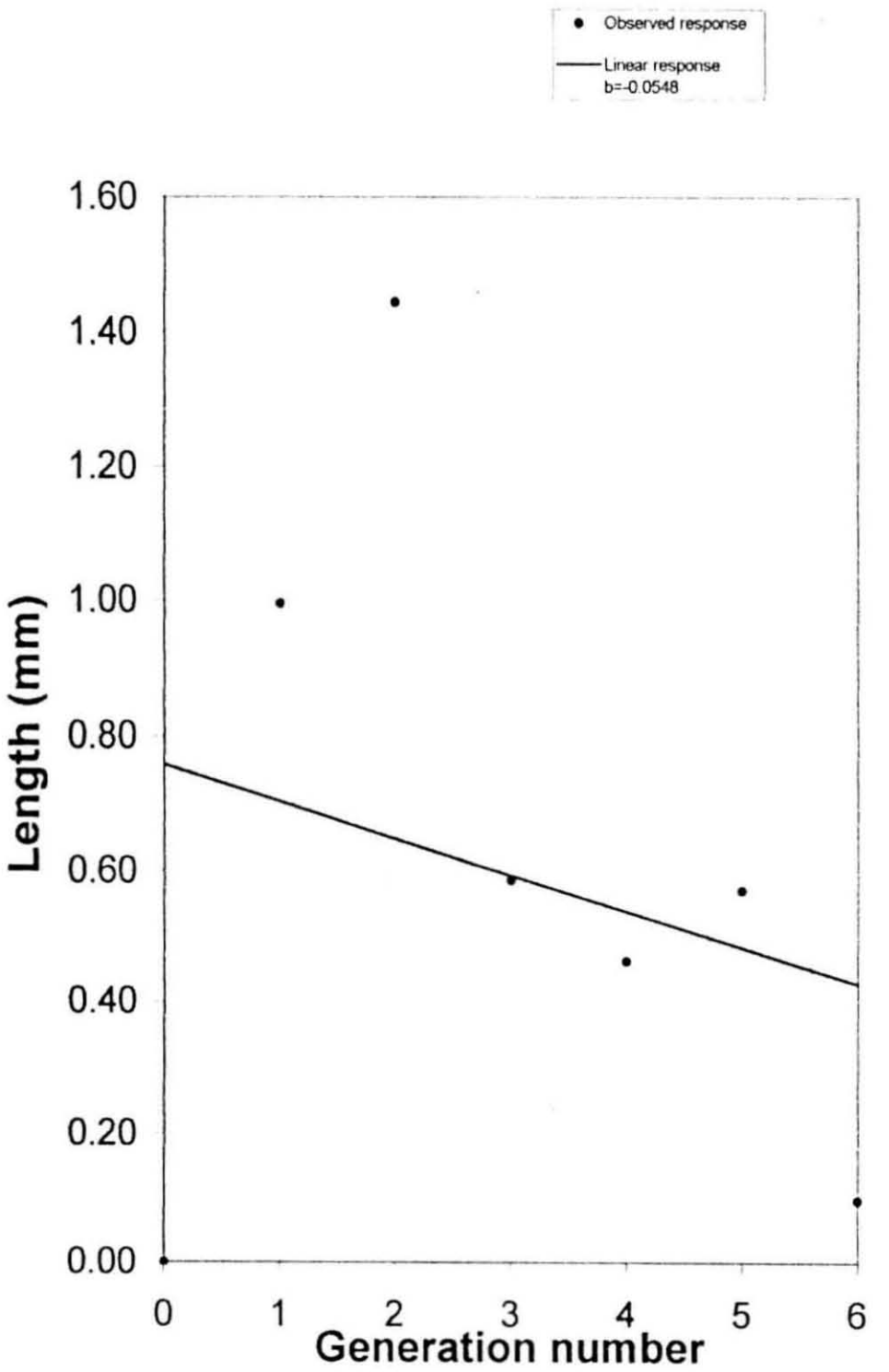


Fig. 15 Linear trend of correlated response in 6-day length of SNS females

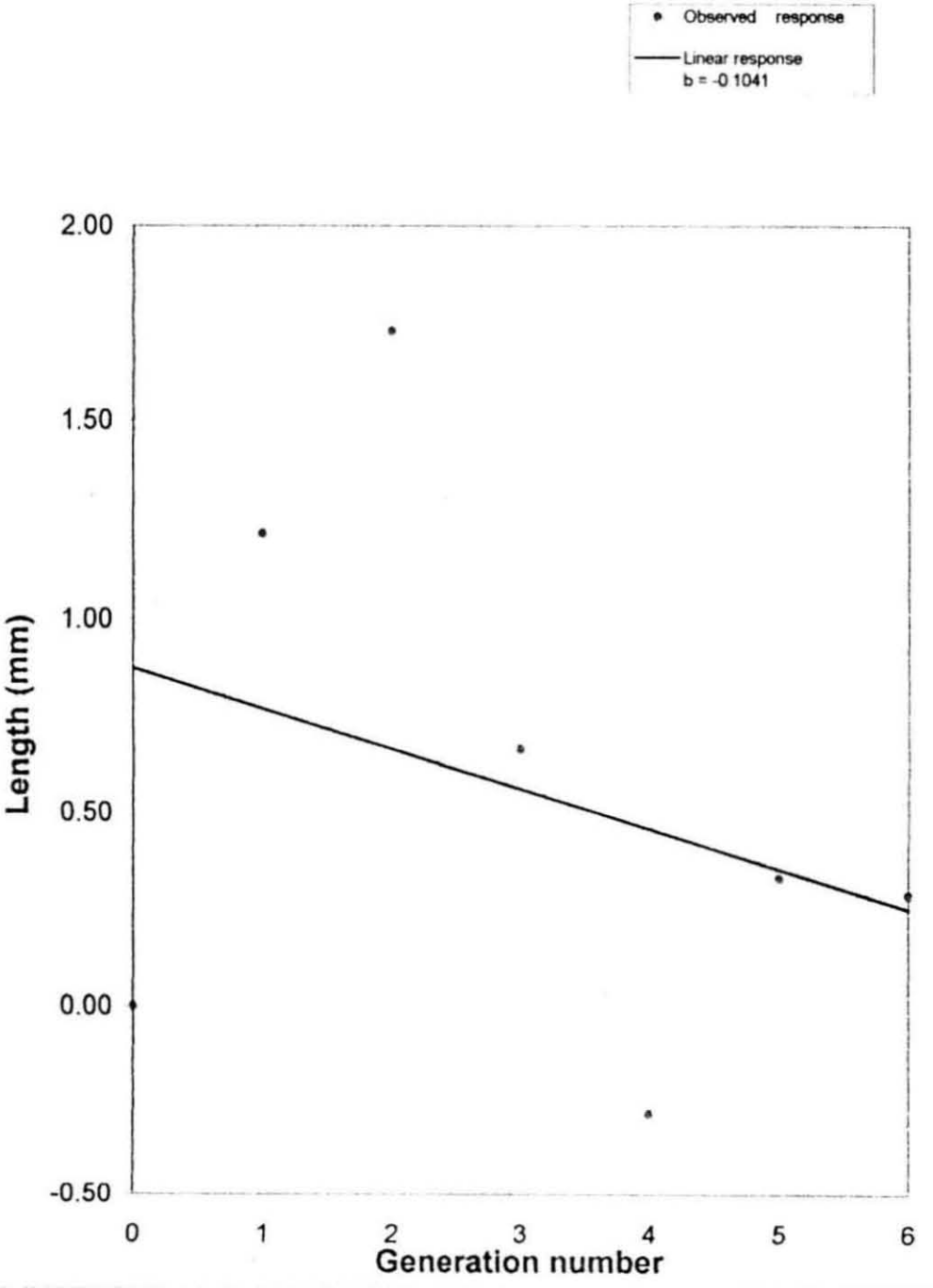


Fig. 16 Linear trend of correlated response in 6-day length of BNS males

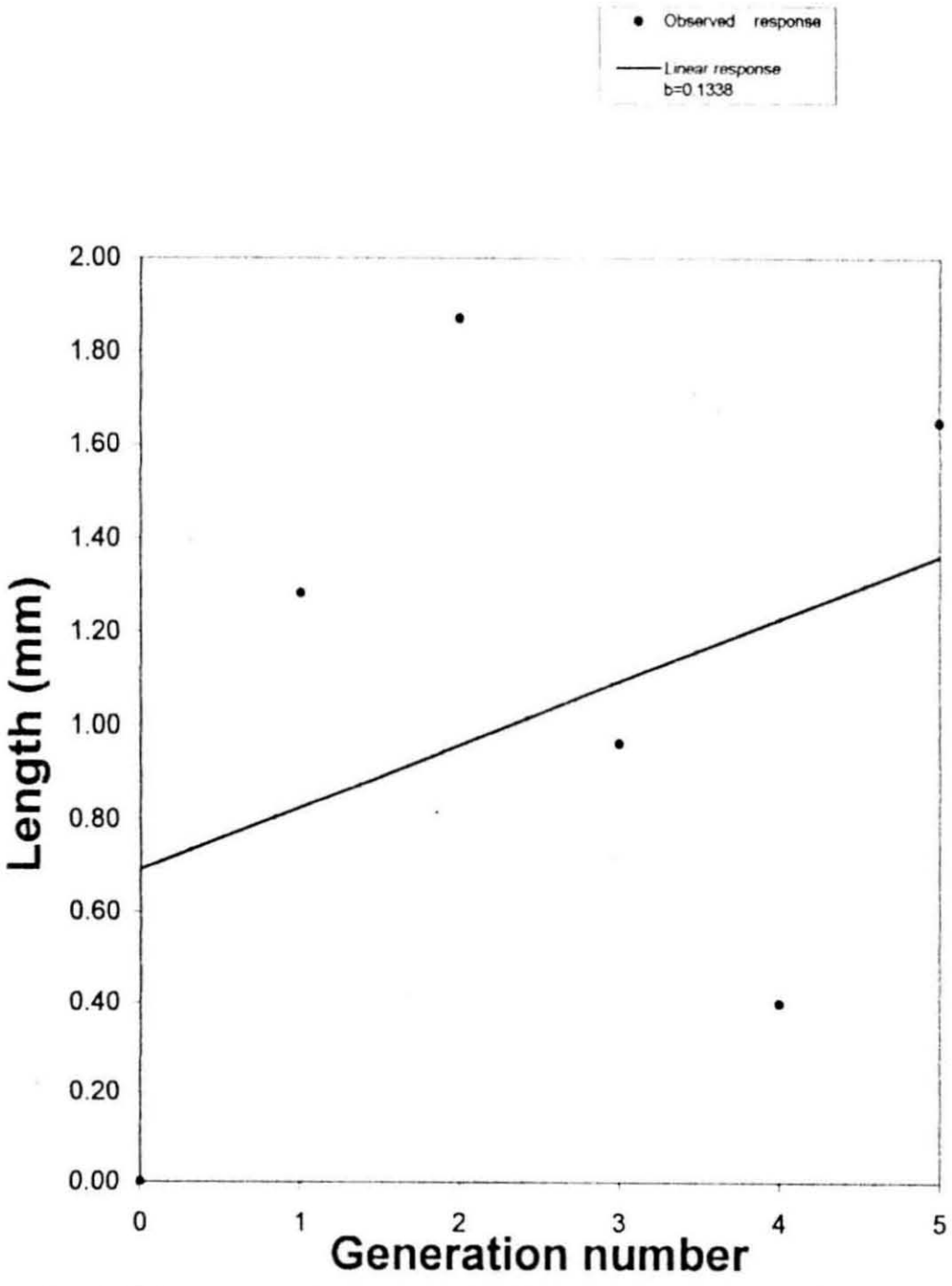
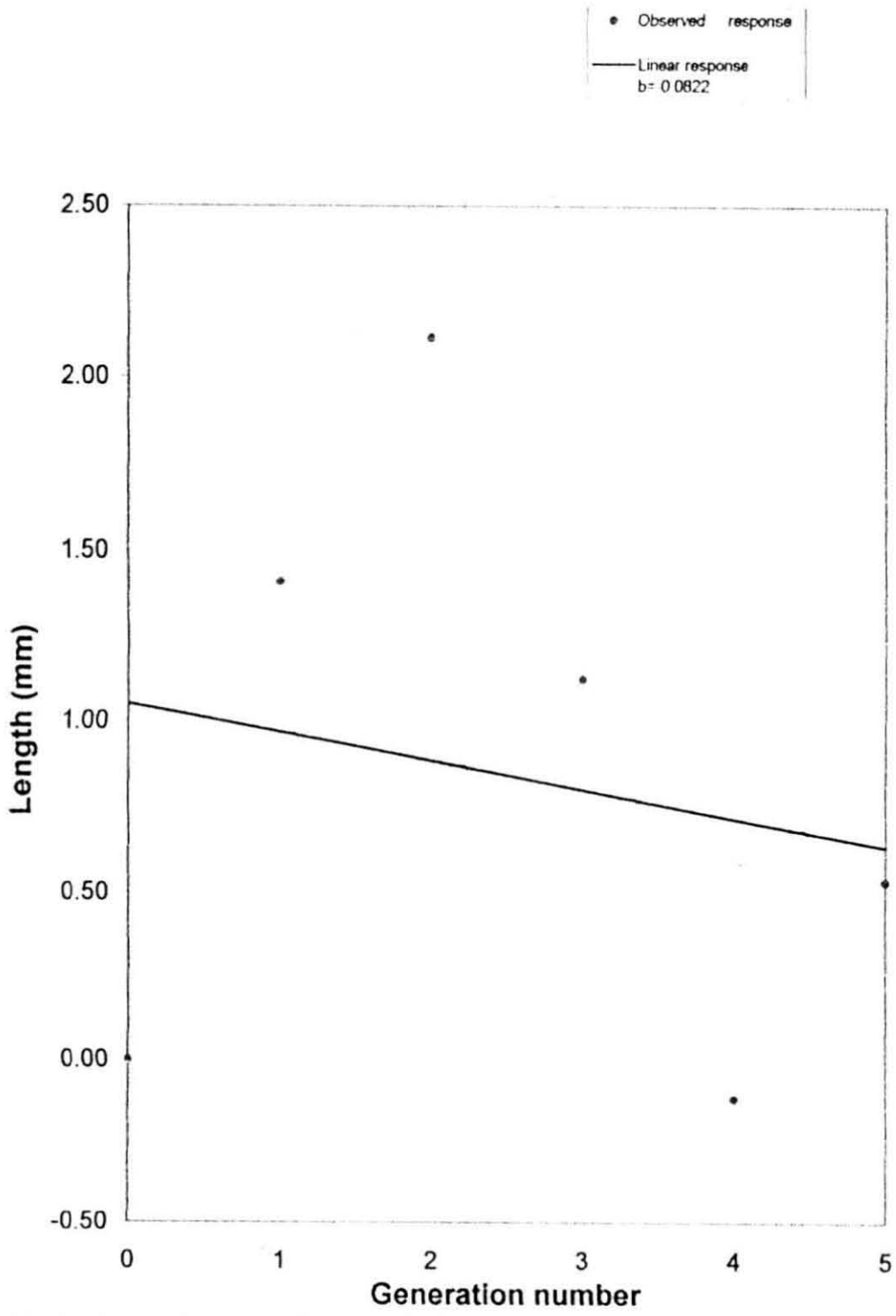


Fig. 17 Linear trend of correlated response in 6-day length of BNS females



length on 6th day showed an increase compared to the base population in both sexes of both lines over the generations. The generation means were tested for significance of difference from base population. In SNS line, all the generation means of both sexes were significantly different, excepting sixth generation males. In BNS line also, means of all generations were significantly different, except the fourth generation females. However, the regression coefficients of generation means on generation numbers were found to be non-significant in both sexes of both the lines. The regression coefficients estimated for males and females were -0.0548 ±0.1006 mm and -0.1041 ±0.1377 mm in SNS line and 0.1338 ±0.1621 mm and - 0.0822 ±0.2036 mm in BNS line. Linear trend in this trait for males and females of both the sexes are shown in Fig 14 to 17.

3.2.1.3 Length at Sexual Dimorphism

The average length at sexual dimorphism in SNS and BNS lines are presented sex-wise for each of the generations, in Table 41. It is seen that though the average length of animals at dimorphism increased in males as well as females of both the lines over the generations, this increase was found to be non-significant. The mean correlated response indicated by coefficient of regression of length at sexual dimorphism on generation numbers were 0.0413 ±0.0273 mm and 0.0147 ±0.0353 mm in males and females respectively, in SNS line. The corresponding values of BNS line were 0.0856 ±0.0555 mm and 0.0359 ±0.0668 mm. The cumulative responses realized in each of the generations are also presented in the Table 41 and Fig. 18 to 21.

Table 41 Mean ($\overline{X}$), Standard deviation (SE) and correlated response of length at sexual dimorphism in SNS and BNS lines.

Line	Generation	Male		Female	
		$\overline{X}$ (mm)±SE	Correlated response	$\overline{X}$ (mm)±SE	Correlated response
SNS	0	3.8004 0.0238	0.0000	3.9053 ±0.0274	0.0000
	1	4.1179 ±0.0332**	0.3175	4.3292 ±0.0434**	0.4239
	2	4.2300 ±0.0262**	0.4296	4.4505 ±0.0318**	0.5452
	3	4.0464 ±0.0219**	0.2460	4.1222 ±0.0240**	0.2169
	4	4.2084 ±0.0391**	0.4080	4.1727 ±0.0361**	0.2674
	5	4.2754 ±0.0377**	0.4750	4.2821 ±0.0261**	0.3768
	6	4.0880 ±0.0265**	0.2876	4.1667 ±0.0348**	0.2614
b±S. E.	-	**0.04130 ±0.0273 NS**	-	**0.0147 ±0.0353 NS**	-
BNS	0	3.8004 ±0.0238	0.0000	3.9053 ±0.0274	0.0000
	1	4.2308 ±0.0376**	0.4304	4.4586 ±0.0512**	0.5533
	2	4.5100 ±0.0334**	0.7096	4.7302 ±0.0378**	0.8249
	3	4.1432 ±0.0249**	0.3428	4.2591 ±0.0304**	0.3538
	4	4.0894 ±0.0369**	0.2890	4.1355 ±0.0508**	0.2302
	5	4.5580 ±0.0488**	0.7576	4.4449 ±0.0317**	0.5396
b±S. E.	-	**0.0856 ±0.0555 NS**	-	**0.0359 ±0.0668 NS**	-

* and ** indicate the significance difference from base population at $P<0.05$ and $P<0.01$ respectively.
NS indicates Not significant

Fig. 18 Linear trend of correlated response in length at sexual dimorphism of SNS males

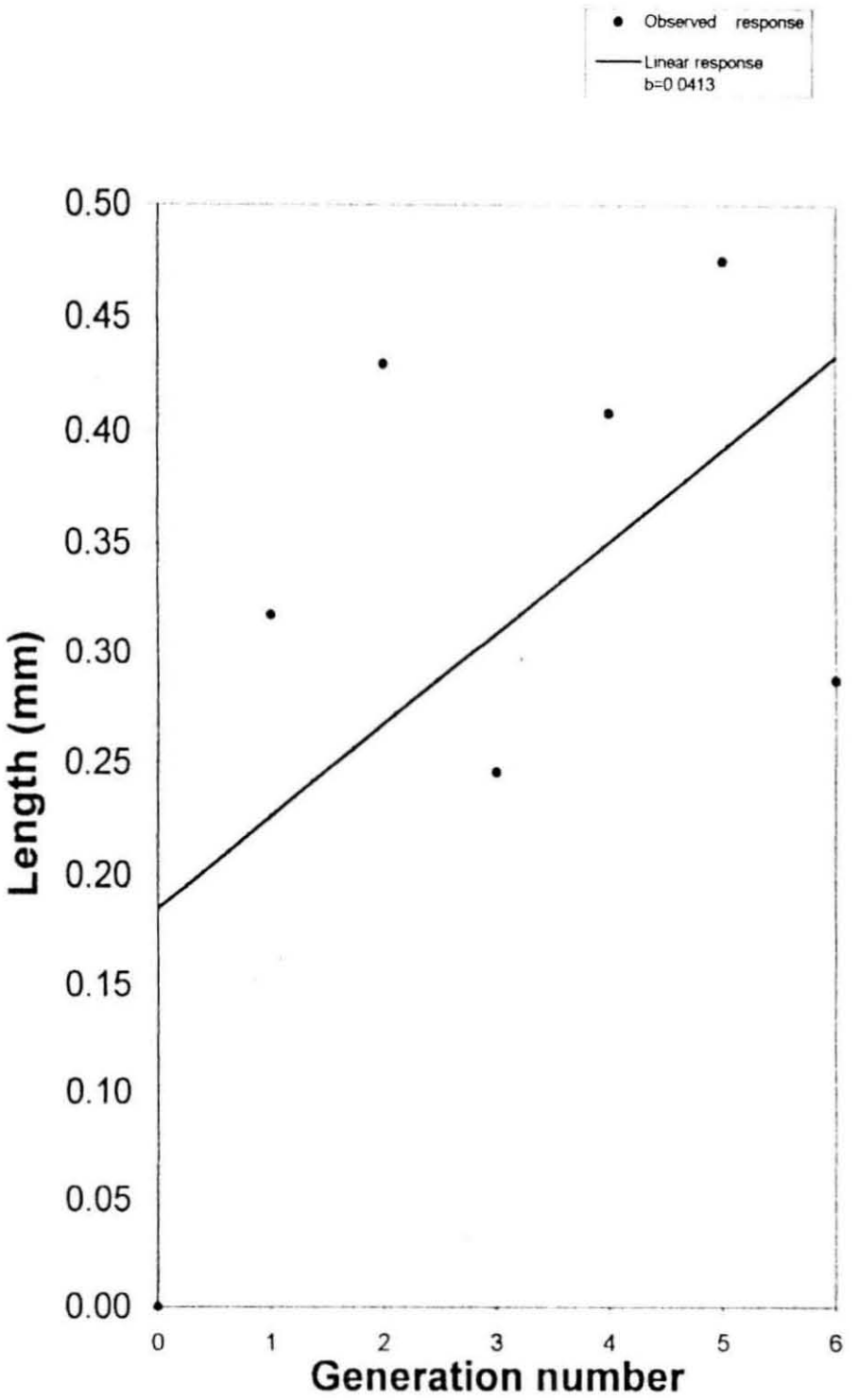


Fig. 19 Linear trend of correlated response in length at sexual dimorphism of SNS females

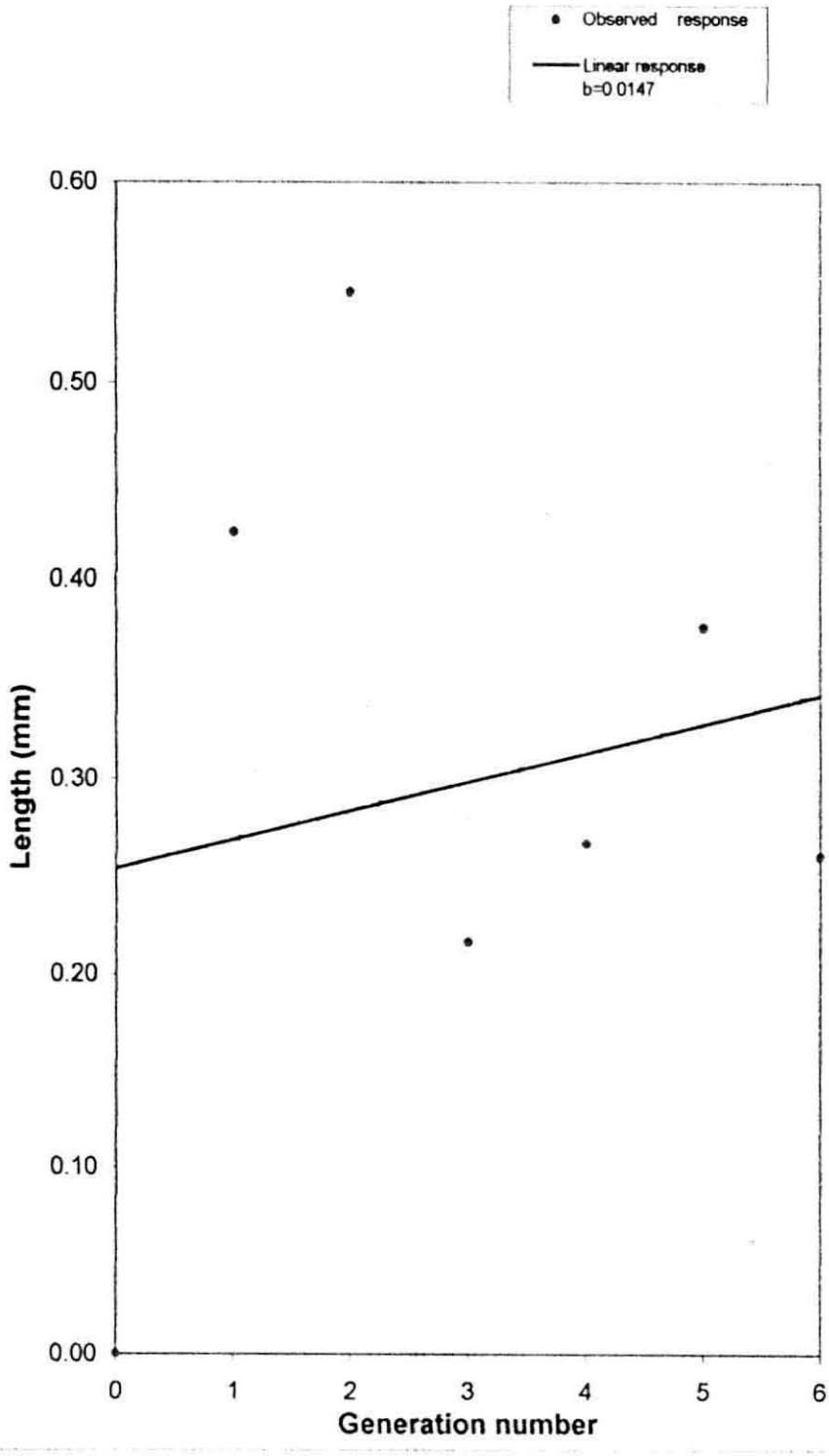


Fig. 20 Linear trend of correlated response in length at sexual dimorphism of BNS males

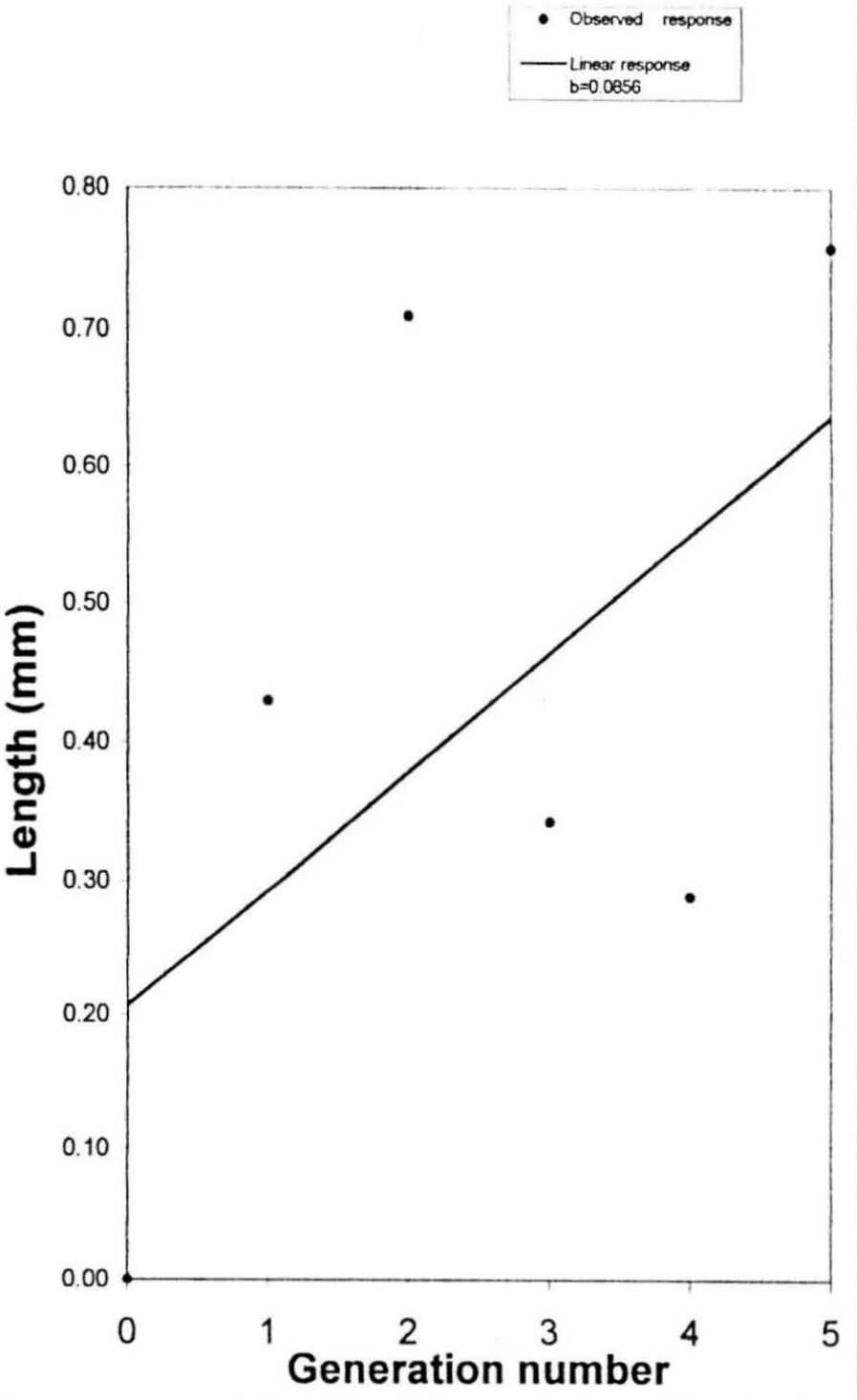
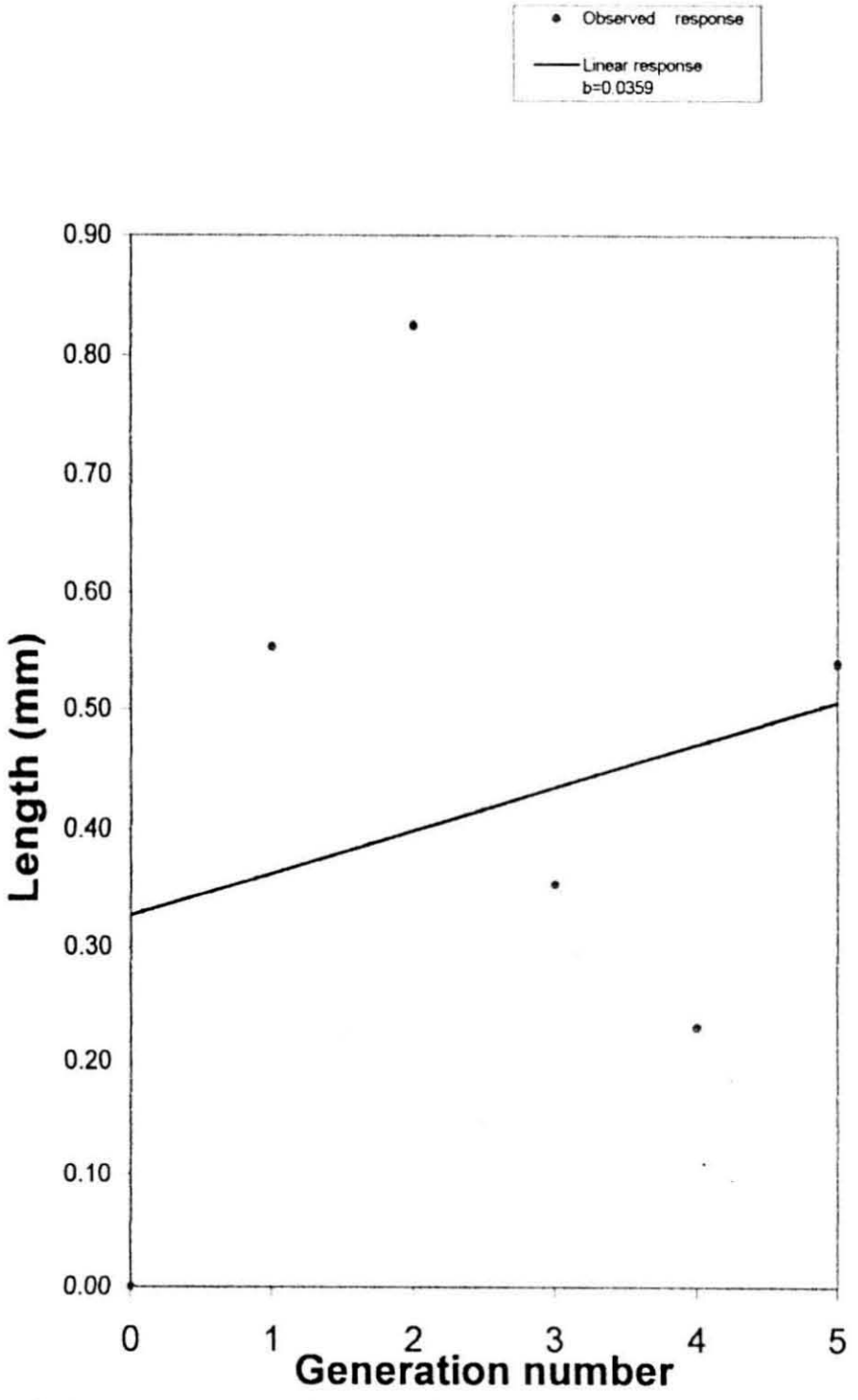


Fig. 21 Linear trend of correlated response in length at sexual dimorphism of BNS females



3.2.1.4 Age at sexual Dimorphism

Although the mean age (days) at sexual dimorphism showed a decrease in selected generations of both the lines as compared to the base population, (Table 42 and Fig 22 to 25) the change was not found to be consistent. The differences were significant in the initial three generations, but were not so in the later generations, except in BNS male.

Average of the generation means were below the base generation mean. The correlated response per generation estimated as regression coefficient of the generation means on the generation numbers, were 0.0756 ± 0.0615 and 0.0708 ± 0.0898 days in males and females respectively of the SNS line. The corresponding values of BNS were -0.02082 ± 0.0076 days and 0.0739 ± 0.1163 days. The correlated responses in age at sexual dimorphism were not significant.

3.2.1.5 Age at first offspring laid

Although the age at first offspring laid showed increase in several generations of both the lines, it did not reveal any definite trend either in the direction or magnitude of the change (Table 43 and Fig 26 & 27). The mean correlated response estimated as the regression coefficient of the age at first offspring laid on generation numbers in SNS and BNS lines were 0.2237 ± 0.2440 and 0.2428 ± 0.3748 days respectively. The mean responses were, however, not significant statistically.

3.2.1.6 Length at first offspring laid

Though the mean length at the time of first offspring laid increased marginally in the selected generation, none of the generations differed

Table 42 Mean ($\overline{X}$), Standard deviation (SE) and correlated response of age at sexual dimorphism in SNS and BNS lines

Line	Generation	Male		Female	
		$\overline{X}$ (Days)±SE	Correlated response	$\overline{X}$ (Days)±SE	Correlated response
SNS	0	5.8861 ±0.0663	0.0000	5.9766 0.2043	0.0000
	1	5.3094 ±0.0546**	-0.5767	5.2602 ±0.0550**	-0.7164
	2	5.1255 ±0.0240**	-0.7606	5.0727 ±0.0173**	-0.9039
	3	5.5265 ±0.0417**	-0.3596	5.3842 ±0.0376**	-0.5924
	4	5.8824 ±0.0948	-0.0037	6.3935 ±0.0913	0.4169
	5	5.7292 ±0.0747	-0.1569	5.8105 ±0.0614	-0.1661
	6	6.0598 ±0.0886	0.1737	5.8305 ±0.0919	-0.1461
b±S. E.	-	**0.0756 ±0.0615 NS**	-	**0.0708 ±0.0898 NS**	-
BNS	0	5.8661 ±0.0663	0.0000	5.9766 ±0.2043	0.0000
	1	5.2246 ±0.0437**	-0.6415	5.2209 ±0.5386**	-0.7557
	2	5.0417 ±0.0136**	-0.8244	5.0376 ±0.0177**	-0.9390
	3	5.3742 ±0.0453**	-0.4919	5.2614 ±0.0423**	-0.7152
	4	5.8923 ±0.1299	0.0262	6.3261 ±0.1303	0.3495
	5	5.2532 ±0.0685**	-0.6129	5.7857 ±0.0454	-0.1909
b±S. E.	-	**-0.0208 ±0.0076 NS**	-	**0.0739 ± 0.1163 NS**	-

* and ** indicate the significance difference from base population at $P<0.05$ and $P<0.01$ respectively.

NS indicates Not significant

Fig. 22 Linear trend of correlated response in age at sexual dimorphism of SNS males

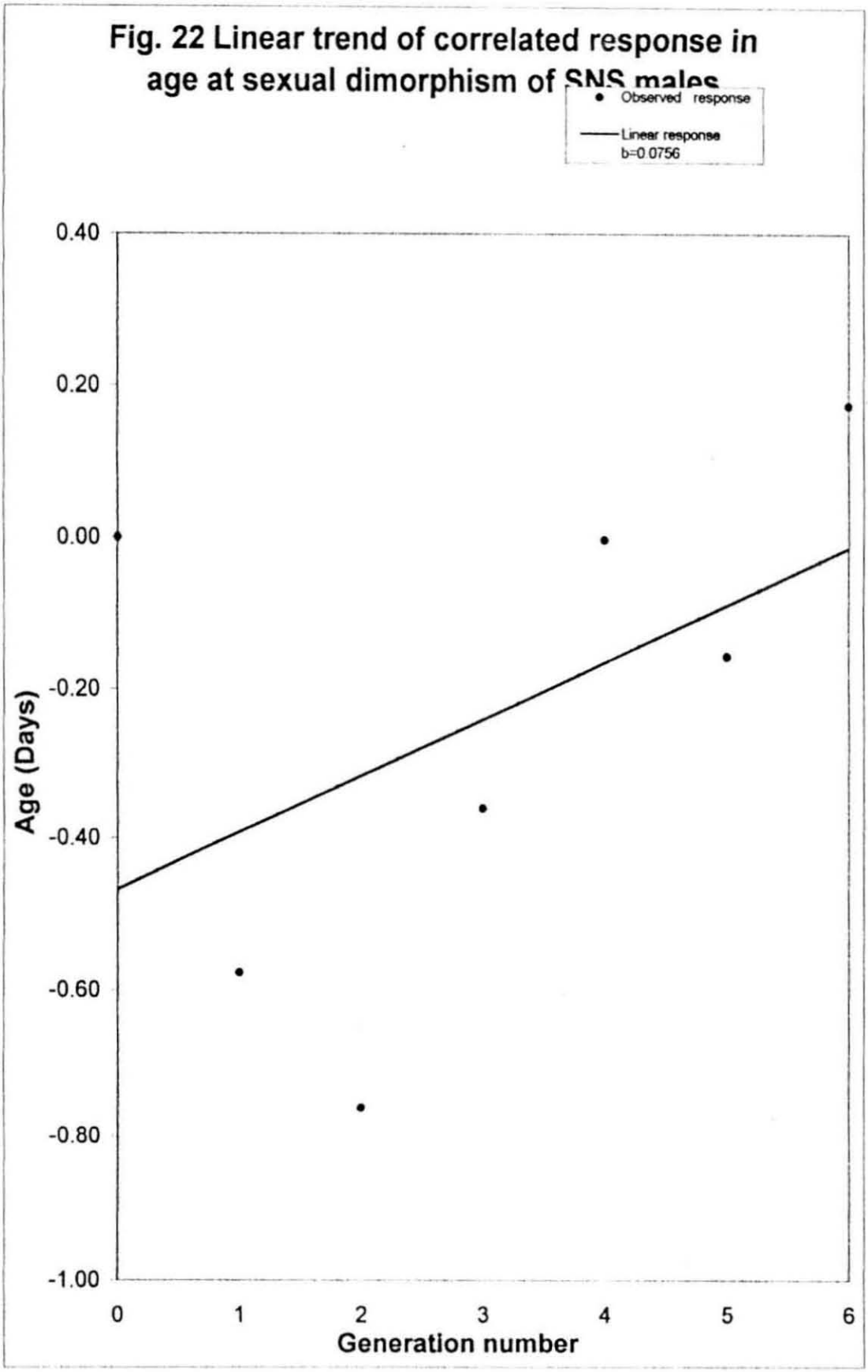


Fig. 23 Linear trend of correlated response in age at sexual dimorphism of SNS females

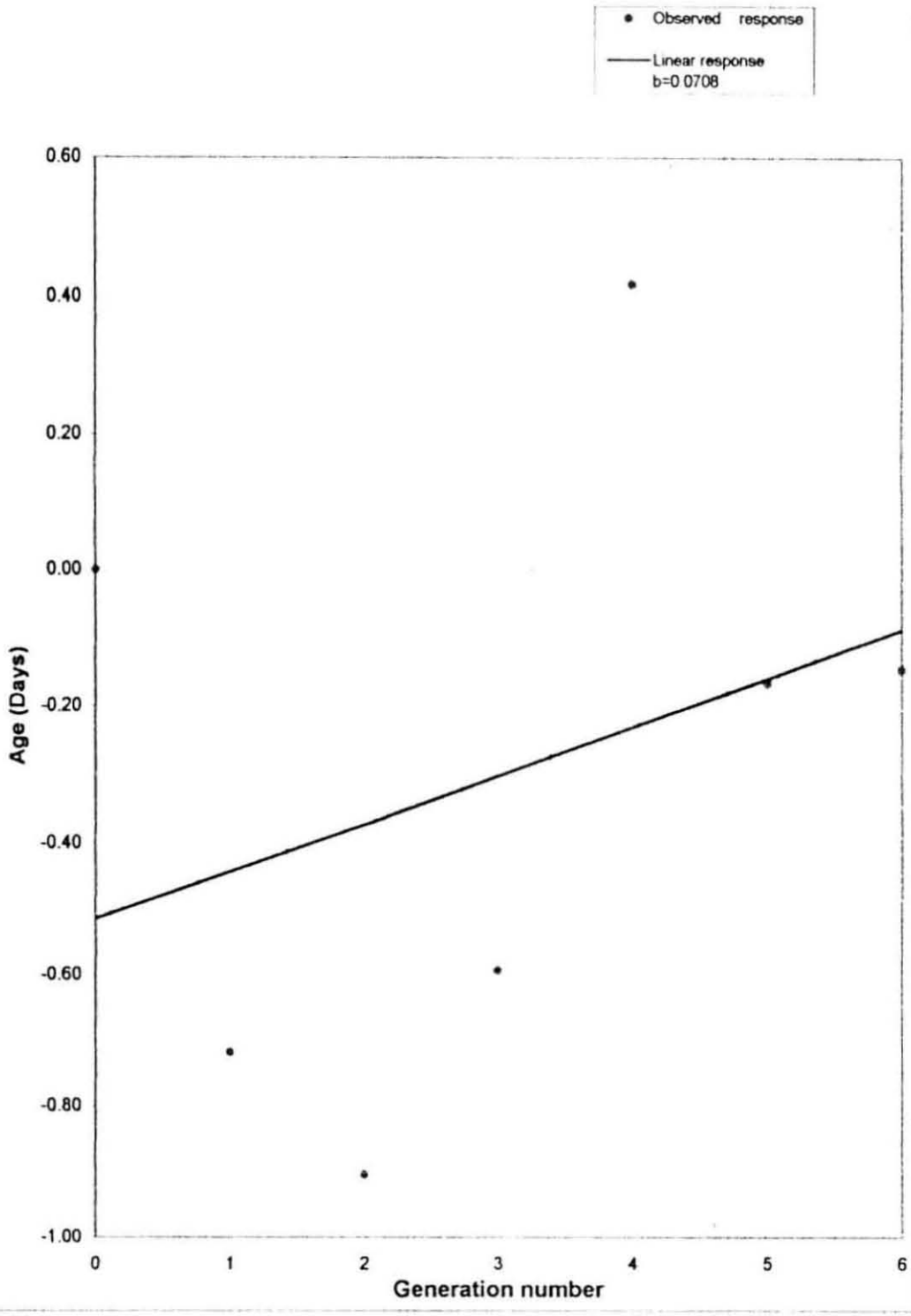


Fig. 24 Linear trend of correlated response in age at sexual dimorphism of BNS males

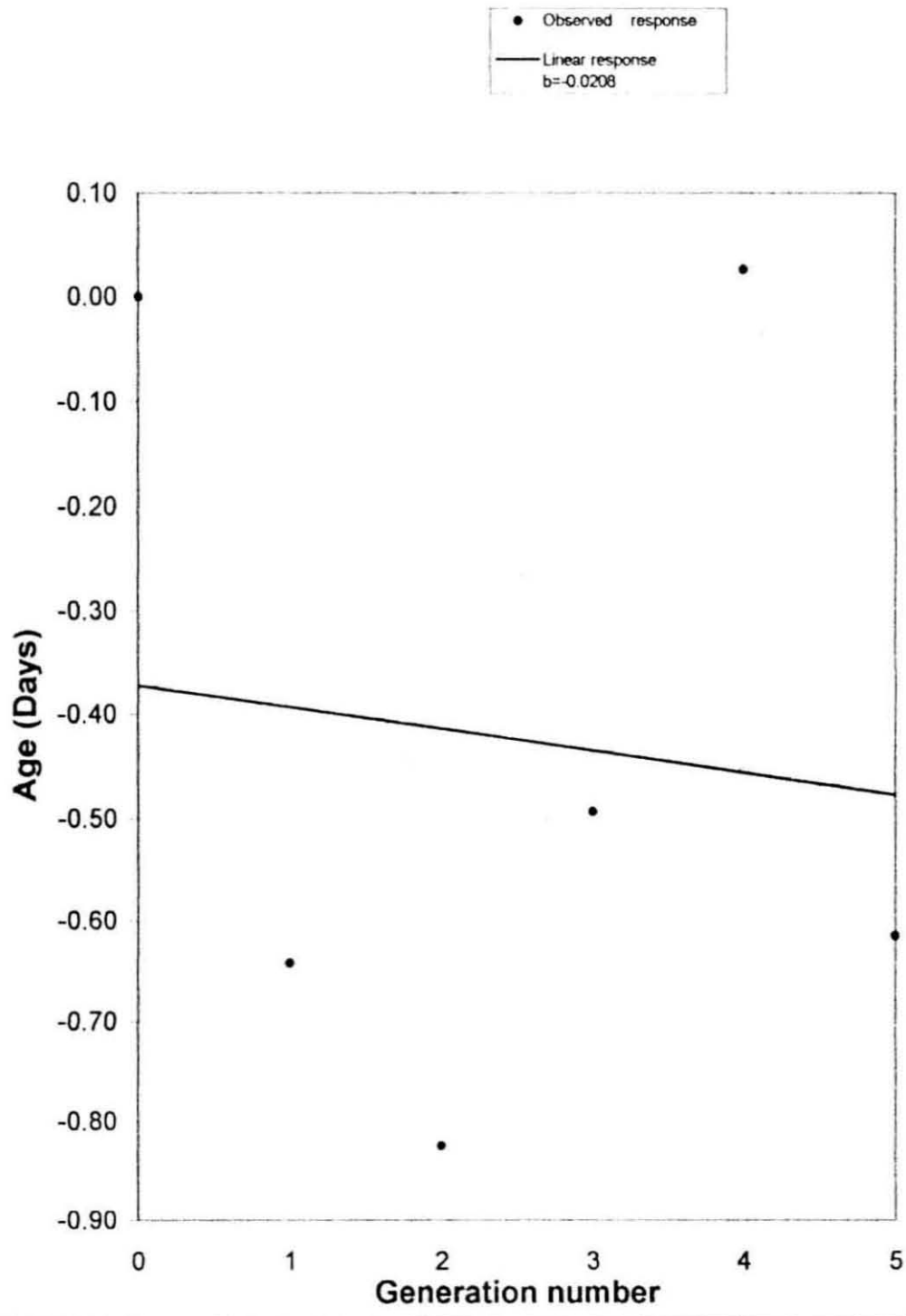


Fig. 25 Linear trend of correlated response *in* age at sexual dimorphism of BNS females

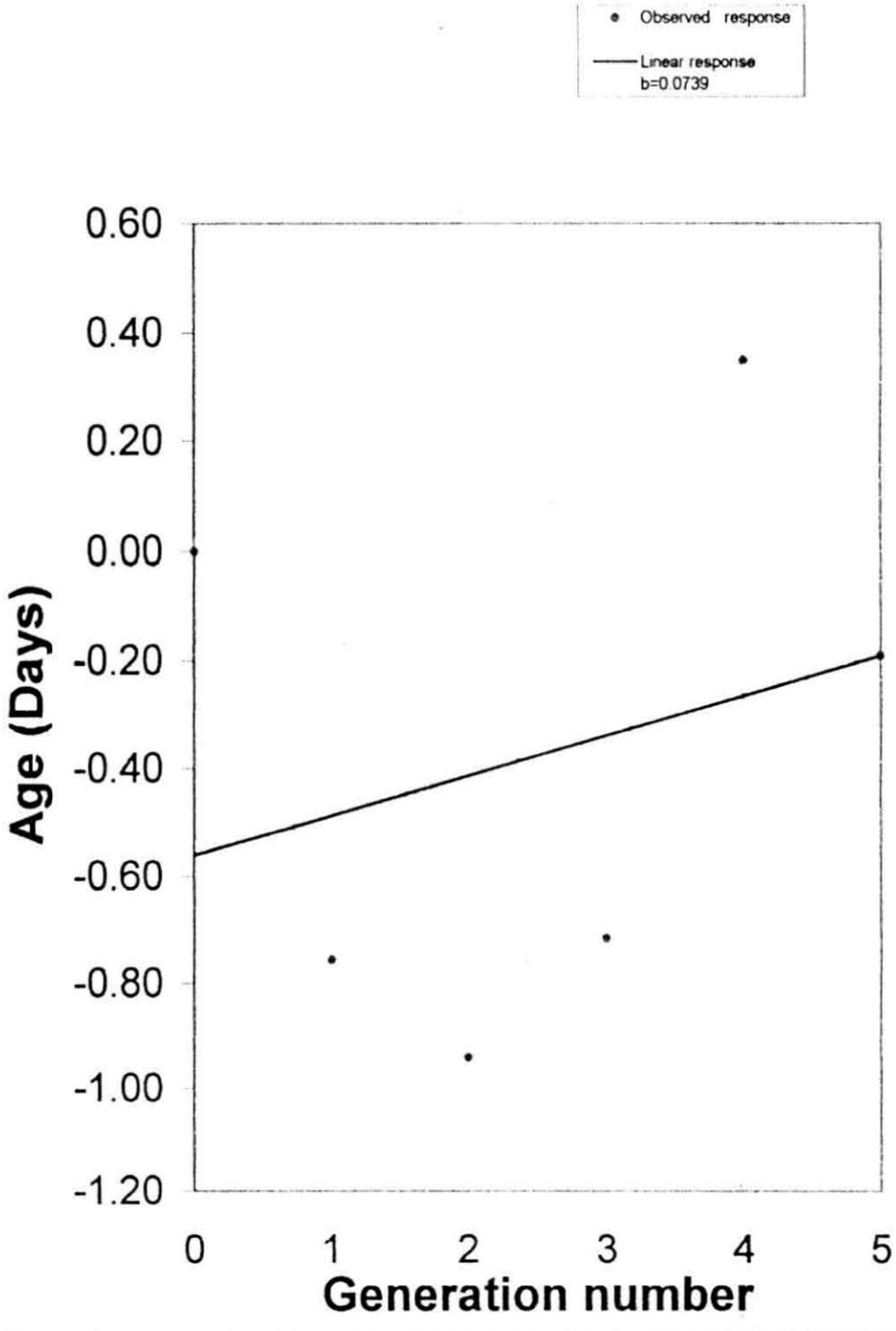


Table 43 Mean ($\overline{X}$), Standard deviation (S.E.) and correlated response of age at first offspring laid in SNS and BNS lines.

Generation	SNS		BNS	
	Female		Female	
	X (Days)±SE	Correlated response	X (Days) ±SE	Correlated response
0	16.0000 ±0.2259	0.0000	16.0000 ±0.2259	0.0000
1	17.9545 ±0.3905**	1.9545	19.0886 ±0.3429**	3.0886
2	16.3718 ±0.3385	0.3718	17.6667 ±0.6915**	1.6667
3	16.0000 ±0.3318	0.0000	15.4688 ±0.5255	-0.5312
4	18.2295 ±0.4326**	2.2295	17.9744 ±0.4726**	1.9744
5	17.4754 ±0.4046**	1.4754	18.8077 ±0.4859**	2.8077
b±S. E.	**0.2237 ±0.2440 NS**	-	**0.2428 ±0.3748 NS**	-

** indicate the significance difference from base population at $p<0.01$.
NS indicates Not significant

Fig. 26 Linear trend of correlated response in age at first offspring laid by SNS females

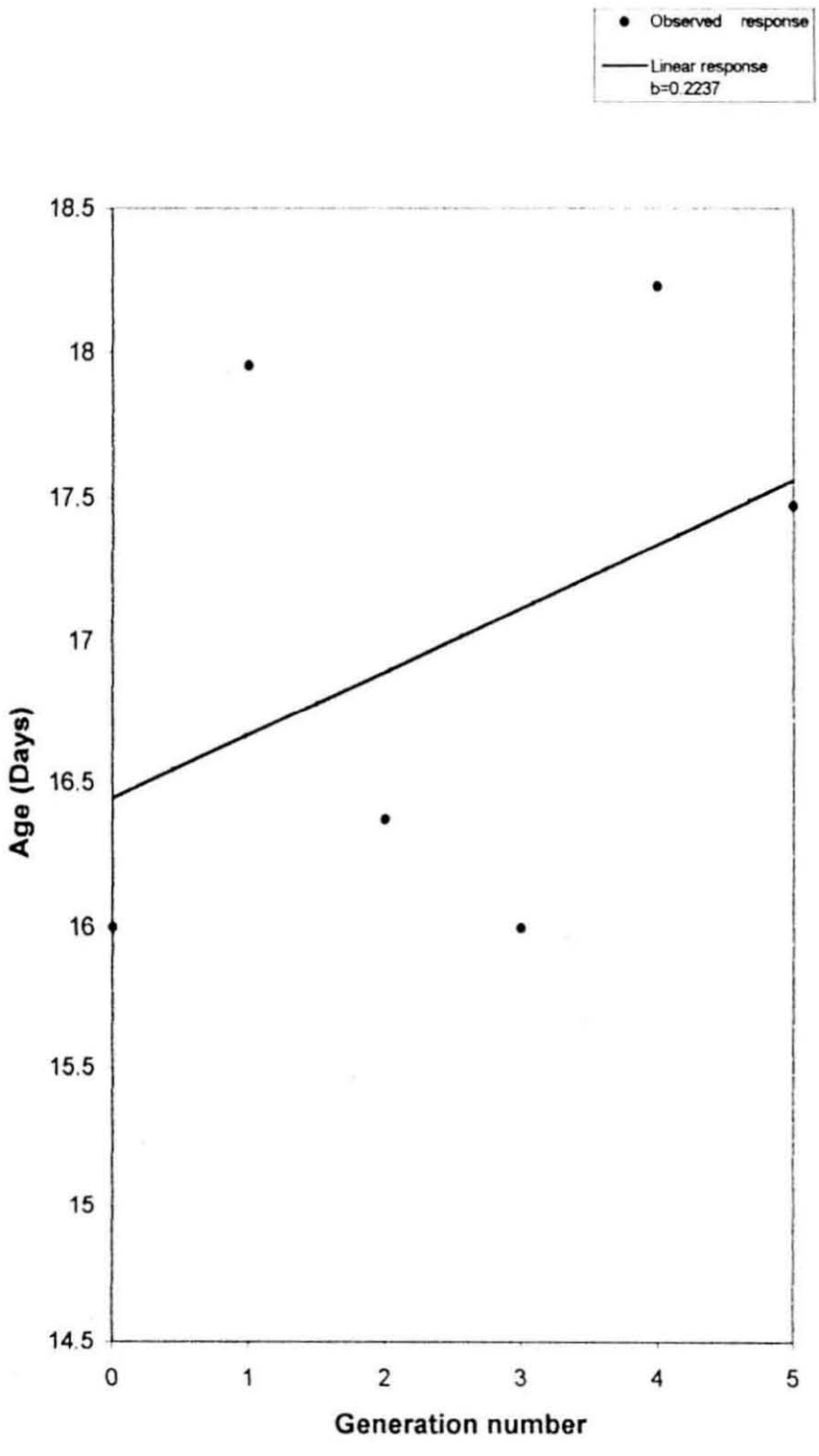
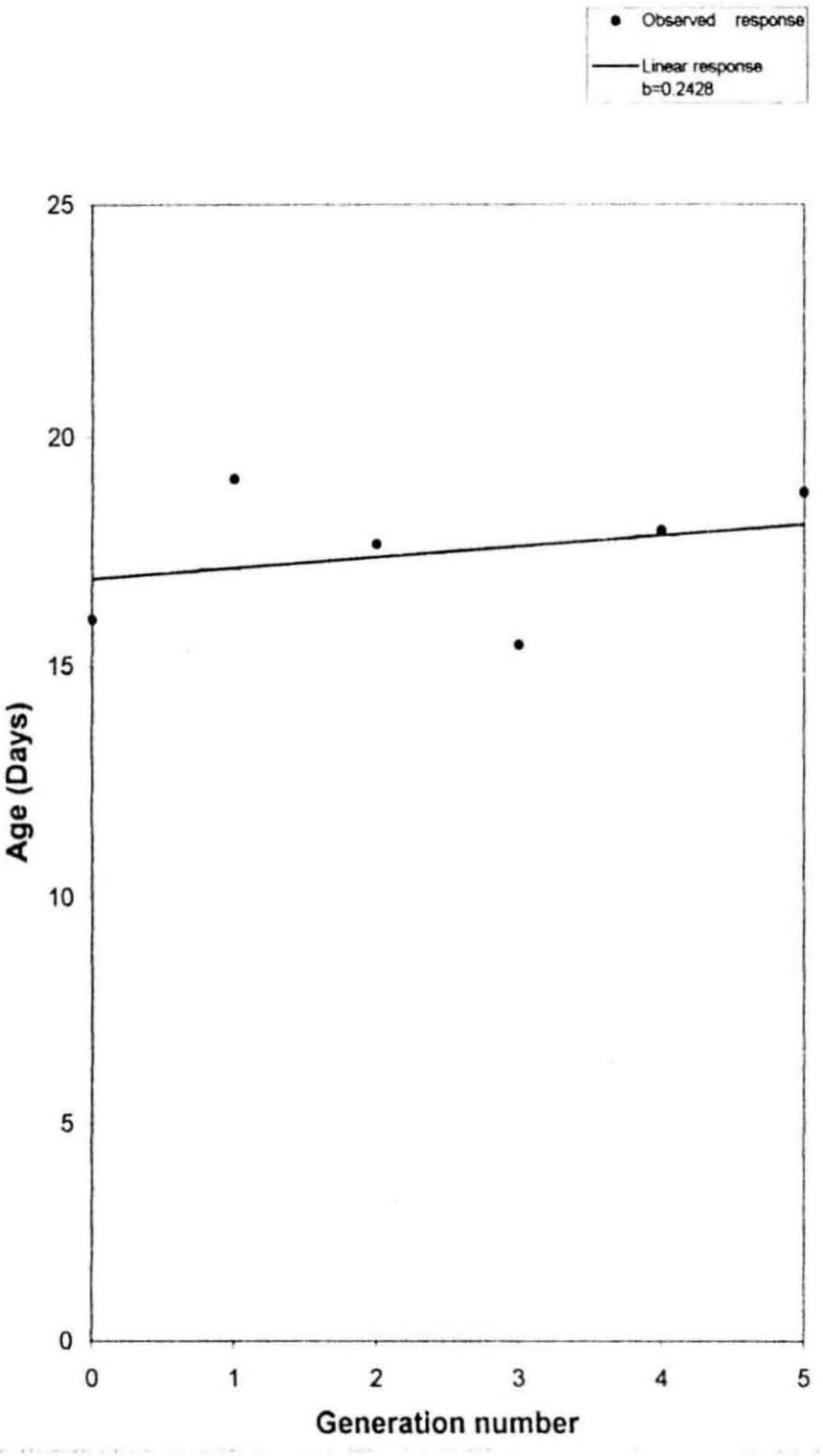


Fig. 27 Linear trend of correlated response in age at first offspring laid by BNS females



significantly from the base population (Table 44 and Fig 28 & 29). After five generations of selection, the mean length of females at the time of first offspring was 10.1184 mm in SNS and 10.6473 mm in BNS line as against 10.0888 mm in base generation. The correlated responses were very negligible and non-significant as can be noted from the regression coefficients, which were 0.0163 ± 0.0297 mm in SNS line and 0.0861 ± 0.0786 mm BNS line.

3.2.1.7 Number of offsprings in the first brood

The mean number of offsprings in first brood and correlated changes in this trait for both SNS and BNS lines are given in Table 45. Linear trend of correlated response in number of offsprings in the first brood by females of both the line is depicted in Fig 30 & 31. Generally, the number of offsprings in first brood showed a substantial decline. The mean number of offsprings laid in first brood declined from 53.5696 ± 1.3675 in base generation to 38.2459 ± 1.3092 in SNS after six generation of selection and to 26.3462 ± 0.8898 in BNS line after five generations of selection. Test of significance for difference between the generation means and base population means were significant in all generations. The mean response was quite substantial as seen from the regression of number of offspring in first brood on the generation numbers, which were -2.4883 ± 1.0412 in SNS line and -4.8971 ± 0.9020 in BNS line. Nevertheless, both the regression coefficients were significant.

The mean values of the lifehistory characteristics such as age at first offspring, time between broods and percentage of encysted offsprings recorded on the completion of selection are presented in Table 46. Total life span was

Table 44 Mean ($\overline{X}$), Standard deviation (SE) and correlated response of length at first offspring laid in SNS and BNS lines.

Generation	SNS		BNS	
	Female		Female	
	X (mm)±SE	Correlated response	X (mm)±SE	Correlated response
0	10.0888 ±0.0854	0.0000	10.0888 ±0.0854	0.0000
1	9.8999 ±0.0910	-0.1889	10.2183 ±0.1137	0.1295
2	9.9895 ±0.1401	-0.0993	10.168 ±0.1398	0.0792
3	9.8388 ±0.1332	-0.2500	9.6686 ±0.1574*	-0.4202
4	10.0913 ±0.1210	0.0025	10.4583 ±0.1963	0.3695
5	10.1184 ±0.1292	0.0296	10.6473 ±0.1608	0.5585
b±S. E.	**0.0163 ±0.0297 NS**	-	**0.0861 ±0.0786 NS**	-

* and ** indicate the significance difference from base population at P<0.05 and P<0.01 respectively.
NS – Non-significant

Fig. 28 Linear trend of correlated response in length at first offspring laid by SNS females

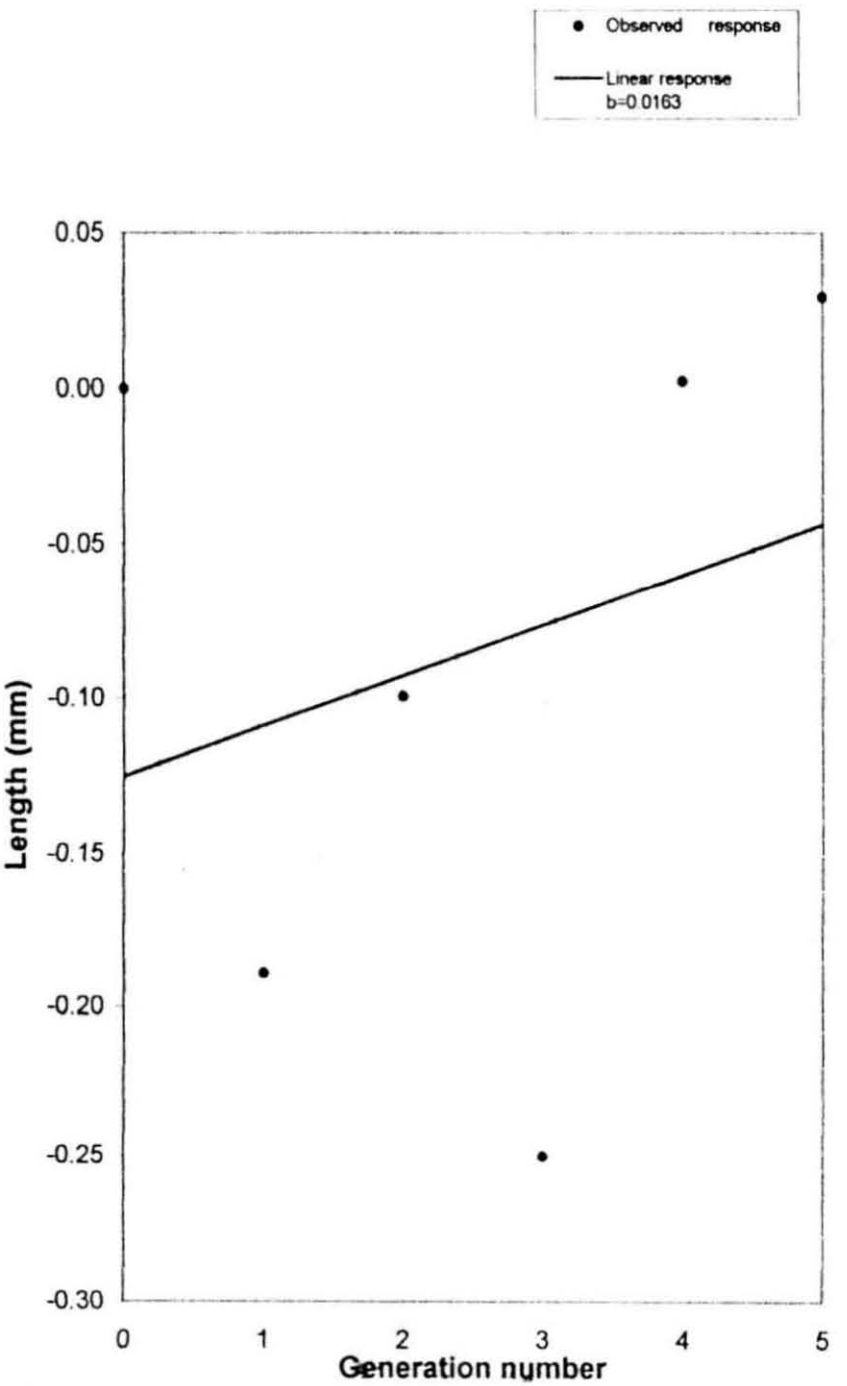


Fig. 29 Linear trend of correlated response in length at first offspring laid by BNS females

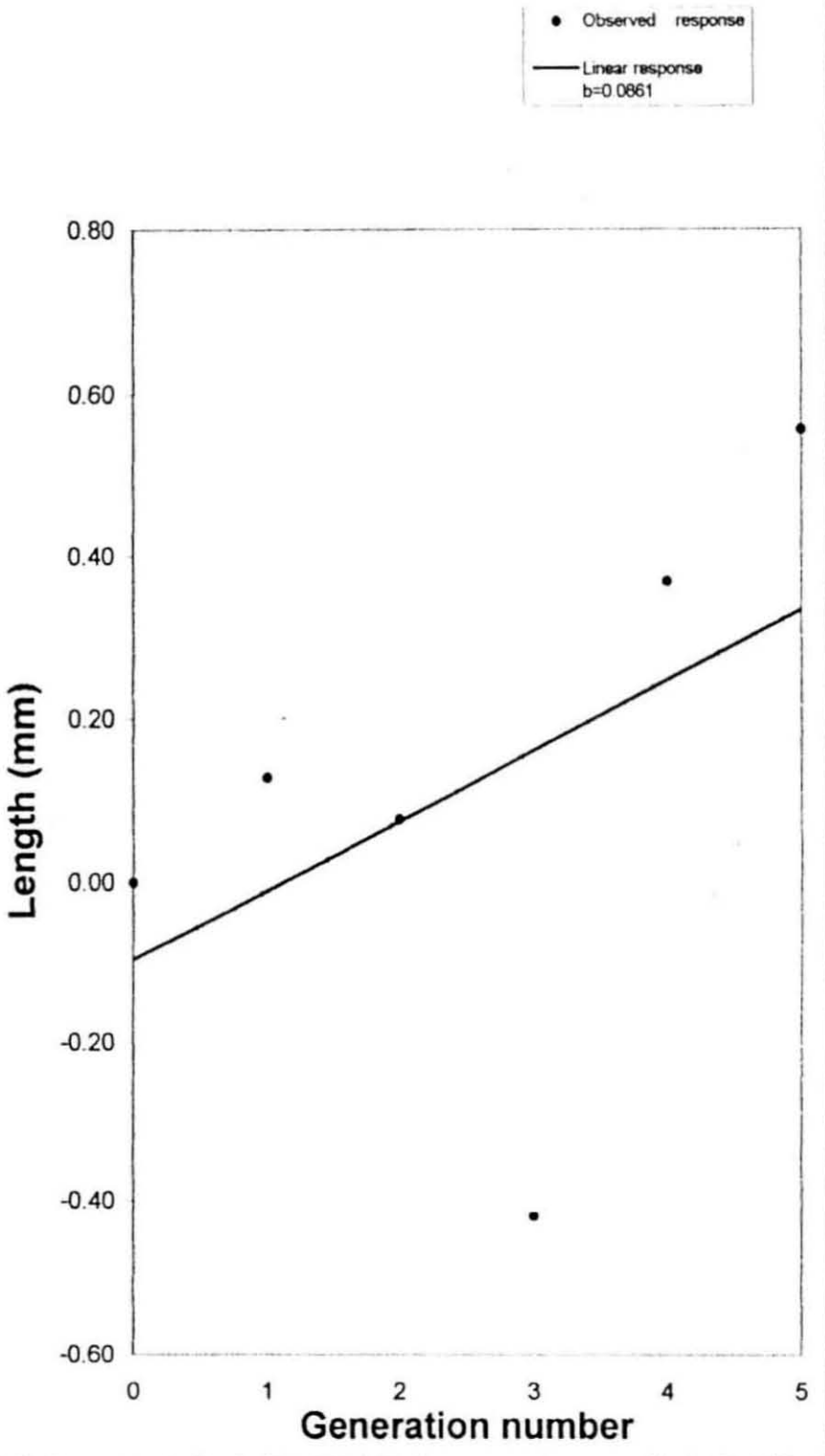


Table 45 Mean ($\overline{X}$), Standard deviation (SE) and correlated response of the number of offsprings laid in first brood by SNS and BNS lines.

Generation	SNS		BNS	
	Female		Female	
	X ±S.E.	Correlated response	X ±S.E.	Correlated response
0	53.5696 ±1.3675	0.0000	53.5696 ±1.3675	0.0000
1	42.6545 ±1.1996**	-10.9151	47.8861 ±1.2026**	-5.6835
2	40.8462 ±1.3690**	-12.7234	37.8413 ±1.1925**	-15.7283
3	36.2708 ±1.4854**	-17.2988	34.2188 ±1.8419**	-19.3508
4	40.6885 ±1.5969**	-12.8811	37.3333 ±1.6090**	-16.2363
5	38.2459 ±1.3092**	-15.3237	26.3462 ±0.8898**	-27.2234
b±S. E.	**-2.4883 ±1.0412+**	-	**-4.8971 ±0.9021++**	-

** indicate the significance difference from base population at P<0.01 .
+ and ++ indicate the significant difference of 'b' at P< 0.05 and P<0.01 respectively.

Fig. 30 Linear trend of correlated response in number of offsprings in the first brood by SNS females

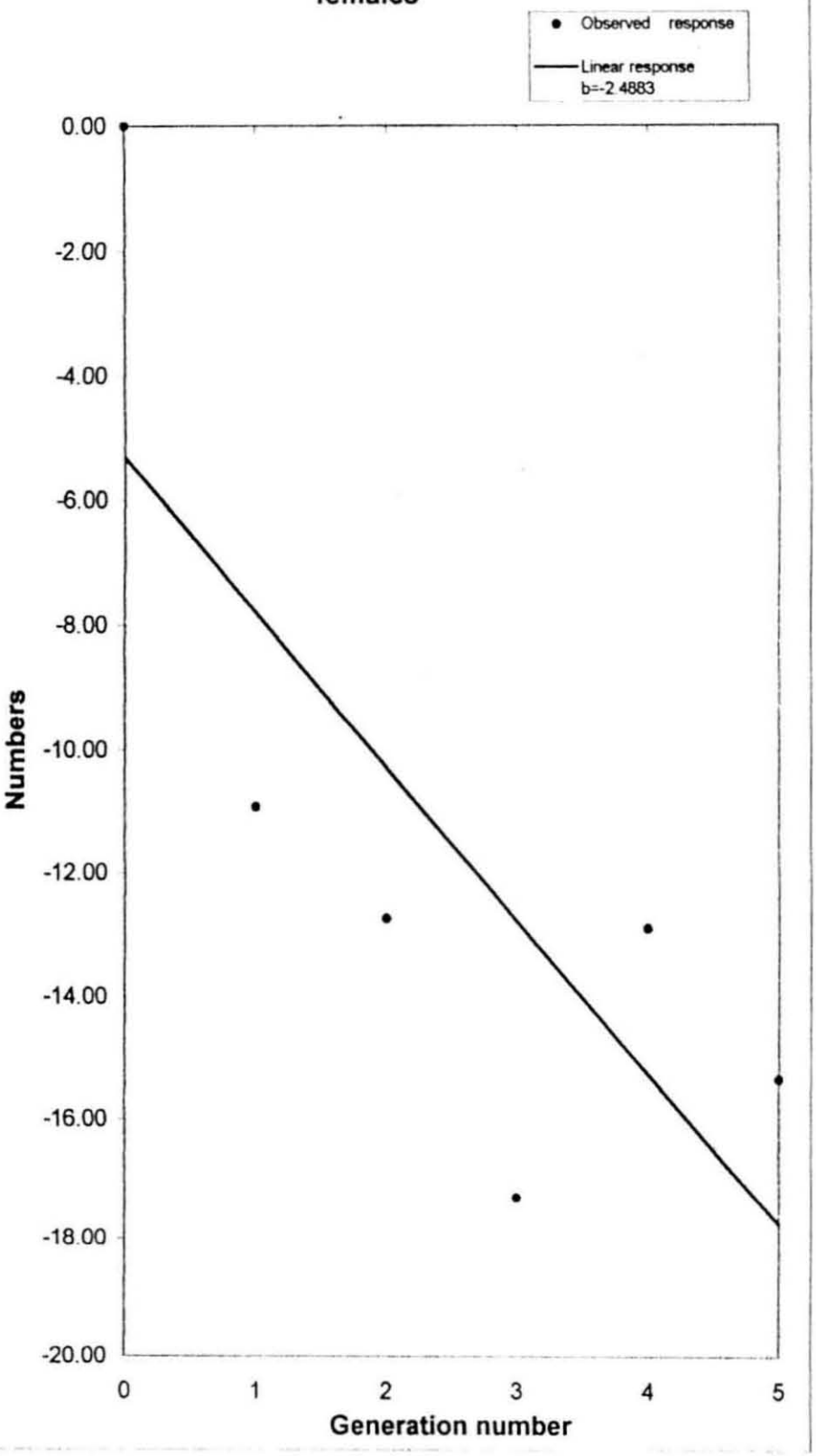
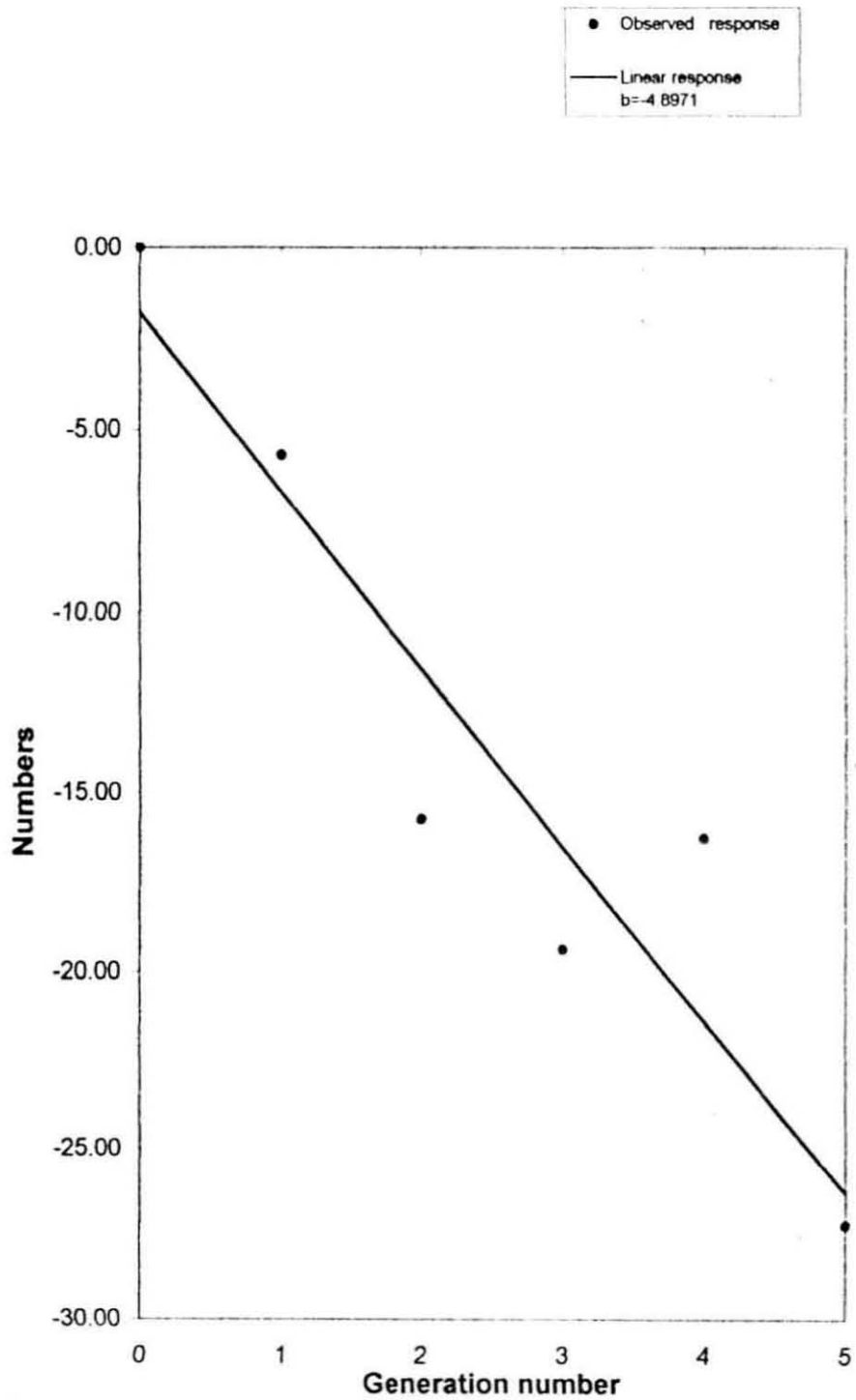


Fig. 31 Linear trend of correlated response in number of offsprings in the first brood by BNS females



50.9091 days in base population, as against 52.74 days in final generation of SNS line and 51.012 days in BNS line. Time between the broods, which was 3.6632 days in base population, changed to 4.21 days in SNS line and 5.00 days in BNS line. No significant change was observed in the percentage of encysted offspring, which was 49.9448 in base population, 51.7444 in the final generation of SNS line and 51.8729 in BNS line.

Female reproductive characteristics such as broods per female, offspring per day per female, total offspring per female, pre-reproductive period, reproductive period and post-reproductive period were also studied (Table 46). Broods per female were 9.0003 in base population as against it was 8.4401 and 6.0907 in the final SNS and BNS populations respectively. Offspring per day per female were 13.6875 in base population, which in final population increased to 14.9601 in SNS, but decreased to 10.5999 in BNS. Total number of offspring produced were maximum in final SNS population (788.9966) but least in final BNS (540.7239) as compared to base population (696.818). Pre-reproductive period increased to 17 days in SNS final population as compared to 15.2121 day of base population. Similarly pre-reproductive period increased to 19 days in BNS final population. Reproductive period was maximum (35 days) in SNS final population but least (30 days) in BNS final population, as compared to 32.9697 in base population. Post-reproductive period was 3.9091 in base population, 4.2021 in SNS final population and 5.0321 in BNS final population.

3.2.2 Expected response in correlated traits

Expected response in correlated traits, due to selection for naupliar length estimated from full sib heritability, is presented in Table 47. Expected response

Table 46 Life history and reproductive characteristics recorded before selection (base generation) and after selection (final generation) in SNS and BNS lines.

Characters	Base population	Final selected generation	
		BNS	SNS
Age at offsprings laid (days)	15.2121	17.2156	19.7892
Total life span (days)	50.9091	52.7400	51.0124
Time between broods (days)	03.6632	4.2100	5.0000
Total Nauplii released	345.7576	380.7348	260.2348
Total cyst released	351.0606	408.2618	280.4891
Total offspring	696.8180	788.9966	540.7239
Percentage of encysted offsprings	49.9448	51.7444	51.8729
Broods per female	9.0003	8.4401	6.0907
Offspring per day per female	13.6875	14.9601	10.5999
Pre-reproduction period (days)	15.2121	17.2156	19.7892
Reproduction period (days)	32.9697	35.5326	30.4536
Post-reproduction period (days)	3.9091	4.2021	5.0321

Table 47 Expected response in correlated traits due to selection of naupliar size, estimated from full sibs heritability.

Traits	Expected response			
	SNS		BNS	
	Male	Female	Male	Female
3-days age	-0.0890	-0.1757	0.1190	0.0495
6-days age	-0.2555	-0.3454	0.1988	-0.5807
Length at sexual dimorphism	-0.0438	-0.1289	0.0879	0.0252
Age at sexual dimorphism	0.1327	0.1935	-0.0472	0.3960
Age at first offspring laid	-	-0.3429	-	2.5770
Length at first offspring laid	-	-0.2809	-	0.7855
Number of offsprings in first brood	-	3.9773	-	-3.3071

in traits like length on 3 days of age, length on 6 days of age and length at sexual dimorphism were negative in both the sexes of SNS line, whereas, they were positive in BNS line, excepting the length on 6 days of age in females. Expected responses for the age at sexual dimorphism were positive in females of both the lines and SNS males, whereas it was negative in BNS males. The expected response in traits like age at first offspring laid in females was negative in SNS line but positive in BNS line. Expected responses for numbers of offsprings in first brood of females were positive in SNS line but negative in BNS line.

Expected responses in correlated traits due to selection for naupliar length, estimated from b_{op} heritability (Table 48), were similar to full sib heritability estimates, in direction but were of lower magnitude.

Table 48 Expected response in correlated traits due to selection of naupliar size, estimated from b_{op} heritability.

Traits	Expected response			
	SNS		BNS	
	Male	Female	Male	Female
3-days age	-0.0118	-0.0123	0.0150	0.0126
6-days age	-0.0302	-0.0862	0.0647	-0.1364
Length at sexual dimorphism	-0.0022	-0.0067	0.0000	0.003
Age at sexual dimorphism	0.0066	0.0378	-0.0148	0.0000
Age at first offspring laid		-0.1438		0.4289
Length at first offspring laid		-0.0394		0.1228
Number of offsprings in first brood		1.2830		-0.8650


DISCUSSION

DISCUSSION

Artemia has gained immense importance in aquaculture, especially as an ideal and nutritious live food for the larval stages. Biologically, it is an interesting material, an atypical animal inhabiting hypersaline conditions and showing both parthanogenetic and sexual modes of reproduction. Genetically too it is a characteristic animal, with high plasticity and natural existence of various ploidy forms. The premises of present study is that, since the size of *Artemia* nauplius is an important criteria for its effective ingestibility, and since there exists wide variations in the naupliar size, there is an urgent need to evolve different lines/strains, with varying size specifications, to suit the specific requirements of cultured organisms, through selective breeding. The need for developing 'mini cyst' for application in aquaculture has been emphasized by Lenger *et al.* (1986). This in turn calls for an in-depth knowledge about the quantitative genetics of *Artemia*, which at present is almost non existing. It is also essential to evaluate the response to selection, before resorting to large scale selective breeding programmes.

The genetic studies in *Artemia* are limited to cytogenetics, genetic diversity in bisexual and parthanogenetic forms, evolutionary divergence and speciation, electrophoretic analysis of isozymes, DNA fingerprinting etc. (Barigozzi and Baratelli-Zambruni, 1982,1983; Abreu-Grobois and Beardmore, 1982; Abreu-Grobois, 1983). There is, however, an apparent lack of knowledge on the quantitative genetic parameters of the *Artemia* populations. Though the

electrophoretic studies (Abreu-Grobois & Beardmore, 1980;1982) have demonstrated the existence of large amount of genetic variations in the gene pool of *A. franciscana* and striking genetic heterogeneity between strains and in some cases within strains, which expresses itself as differences in morphology (Amat, 1980) and in a number of fitness characteristics(Gajardo & Breadmore,1989; Zapata *et al.* 1990; Browne and Bowen, 1991) there has been no attempt to properly quantify the variability, by estimating the genetic and phenotypic portions of the variance and heritability estimates. Such estimates, along with phenotypic parameters, are vital pre-requisites for formulating both selection and breeding strategies (Simon, 1970).

PHENOTYPIC PARAMETERS

The mean length of base population nauplii in the present study was 486.9912 ± 2.1136 μm in male and 490.5754 ± 1.8157 μm in females. These values are well within the range of naupliar sizes reported by Vanhaecke & Sorgeloos (1980a) for *A. franciscana*. The mean naupliar lengths reported by them are 489 μm and 486 μm in two samples of the population *viz.* GSL1 and GSL2 respectively. It can be noted from the values presented above that the size variation between sexes starts right at naupliar phase itself. The females tend to be larger as compared to males, and this difference in size between sexes increased with age. On 3rd day of age, females were measuring 1.8712 ± 0.0270 mm as against 1.8679 ± 0.0275 mm of males. The recorded mean length on 6th days of age in males and females were 4.1005 ± 0.0754 mm and

4.2990 ± 0.0793 mm respectively as against the mean length of 3.22 ± 0.61 mm reported by Tobias *et al.* (1980) in *A. franciscana*. Vanhaecke & Sorgeloos (1980b) reported the average larval length on seven days of age to be 3.16 ± 0.17 mm for the San Francisco Bay strain and stated that Great Salt Lake, Utah strain showed 125 % more growth (i.e. 3.95 mm) than the San Francisco Bay strain. The mean lengths of combined sexes observed in the present study results are comparable with that of the Great Salt Lake, Utah strain. This is quite natural, since the same strain has been used in the present work. The mean length at sexual dimorphism recorded in the present study was 3.8004 ± 0.0238 mm and 3.9053 ± 0.0274 for males and females respectively. The mean age at sexual dimorphism was found to be 5.8861 ± 0.0663 days for males but 5.9766 ± 0.2043 days for females. It can be seen from the results that males reached sexual dimorphism at an earlier age and at a lesser length as compared to females. The age (16.00 ± 0.2259 days) and length (10.0888 ± 0.0854 mm) of female at first offspring laid as well as the total number of offsprings in first brood (53.5696 ± 1.3675) compares sufficiently well with standards values of the natural stock of *A. franciscana*.

GENETIC PARAMETERS

Heritability of the selected trait

Heritability of the trait under selection i.e. naupliar size (length) was estimated using two of the standard procedures *viz.*, (1) regression of offspring on parent and (2) analysis of full sib data.

The estimates from regression of offspring on parents were of medium magnitude and within normal limits, while those from full sib data were generally beyond the normal limits in most of the cases. The pooled estimates of heritabilities from parent offspring regression were 0.2123 and 0.3885 for males and females respectively in SNS line, and the corresponding values in BNS were 0.5777 and 0.3364 respectively (Table 8). The pooled heritabilities estimated from full sib data were 1.3256 in males and 1.1004 in females of SNS while the corresponding values in BNS were 1.2580 and 1.4221 respectively (Table 9).

Heritability estimates from full sib data is the heritability in the broad sense, and is the ratio of the total genetic variance to the total phenotypic variance. The total genetic variance includes additive genetic variance, variance due to dominance deviation and epistatic interaction. High heritability values recorded from full sib data, *vis-à-vis* the parent offspring regression, may be due to a substantial quantum of dominance deviation and / or epistatic interaction in the population under study.

Maternal effects and genetic differences among families also can result in an inflated heritability estimate from full sib data (Lester, 1988). The higher estimates obtained in the present study are on similar lines to those reported by Lester (1988) for early growth in a penaeid *Penaeus stylirostris*. The heritability of early growth, estimated from full-sib data in his (Lester, 1988) Experiments I and II respectively were 1.31 ± 0.62 and 1.27 ± 0.53 for protozoea I, 1.09 ± 0.81 and 0.64 ± 0.58 for Mysis I and 0.84 ± 0.79 and 1.02 ± 0.60 for Post larvae I. He concluded that heritability estimates from full sibs data are most likely to be affected by maternal effects and genetic differences among families and there is

no way that the two causative factors can be separated when dealing with full-sibs.

Another point, which needs to be considered, is that *Artemia* is an atypical animal with lower phylogenic position i.e. less evolved, compared to higher vertebrates, plants etc. in which heritability estimates are always within the theoretical range. Aquatic animals are ectothermic, and lack sophisticated endogenous homeostasis like mammals and birds (Wickins, 1981). As such environment has a profound effect on their phenotypic expression. This may be one of the reasons why the estimated heritability values are higher than normal limits. In the present study, the heritability was estimated from animals which were maintained in identical environment and management practices, under laboratory conditions, excepting for the factor of ambient temperature. This was so became, the experimental period was spread over all the seasons *viz.* Summer, Monsoon and Winter. Since the heritability estimates from full sib data are affected by environment, the above factor might have also contributed to its higher magnitude, as compared to those estimated from parent-offspring regression, which were free from environmental effects. Experimental evidence for the variations in heritability estimates emanating from environmental factors like temperature are available in copepods also. McLaren (1976) estimated the heritability of adult size of copepod (*Eurytemora herdmany)* as 0.0 for male at 10°C and 0.97 at 15°C. This shows that, heritability estimates of growth character are influenced a lot by environmental factor like temperature. Malecha *et al.* (1984) estimated the heritability in broad sense for growth of the juveniles

of the prawn *Macrobrachium rosenbergii* as 0.35 for females and 0.0 for males, and concluded that the heritability estimates for growth have sex-linkage.

The effect of environment on estimates of heritability has already been proved by Hedgecock *et al.*(1976) and Hedgecock & Nelson (1978) in the American lobsters, wherein the estimates were 0.30 without environmental treatment, but 0.38 with temperature treatment. Fairfull *et al.* (1981) reported heritabilities ranging from 0.15 to 0.62 for size at specific moult over different diet treatments in the American lobster.

In the present study, although, the generation-wise and sex-wise estimates of heritability indicated variations, they do not seem to follow any specific trend, as already reported by Dempster and Lerner (1951); Dempster *et al.* (1952); Falconer (1955) and Friars *et al.* (1962). This was true for both sexes, irrespective of the method of estimation.

The regression of heritability estimates on generation number, which is known to indicate mean change in heritability per generation, also did not reveal any specific trend. Evidence of change in the genetic variations within the populations under selection, as manifested by changes in heritability estimates, was reported to be positive by Scosseroli (1957) in *Drosophila malanogaster*. On the other hand, workers like Yamada *et al.* (1958); Gowe (1970); Poggenpoel & Erasmus (1978) etc. reported negative trends. Fairly constant estimates of heritability over the generations, for other terrestrial animals, were reported by geneticists like Dempster & Lerner (1951); Dempster *et al.* (1952); Falconer (1955) and Friars *et al.* (1962). Changes in genetic variance, due to selection

pressure, appear to be controlled by specific genetic constitution of population at the commencement of selection.

Compared to very high heritability of 0.98 for body weight in the copepod *Pseudocalanus*, estimated by McLaren & Corkett (1978) using parent-offspring regression, the heritabilities in *Artemia* nauplii estimated in the present study using the same method were of medium magnitude.

As mentioned earlier, pooled heritability estimates for naupliar length of both SNS and BNS lines by parent-offspring regression were within normal limits, and of medium magnitude, unlike the estimates from full sib data. This is very much on the expected lines, since heritability estimates from parent-offspring regression is the heritability in the narrow sense, which includes mostly additive genetic variance, very little epistatic variance and no dominance variance. Further, these estimates are free of the environmental sources of covariance, since the parent and offspring are usually measured over different time periods. Hence, the estimate from regression of offspring on parent is bound to be more reliable than the estimates from the full sib data.

It is clear from the heritability estimates in the present work that there is profound genetic effect on naupliar length of *A. franciscana*. It also indicates that a substantial portion of the variance in the population is due to additive genetic variance, which can be exploited through a simple mass selection. The higher estimates of full sib heritability highlight the importance of non-additive genetic factors contributing to the variability.

Heritability of the unselected traits

The heritability estimates of unselected traits from parent-offspring regression as well as from full sib analysis showed a similar trend as that of naupliar size (Table 10 – 23). While the heritability estimates from full sib data were beyond normal limits in both the sexes of SNS and BNS lines, those from parent-offspring regression were generally within the normal range. The probable reasons for very high estimates from full sib data have been already discussed in the context of the heritability of naupliar size. Heritability values beyond normal limits reported in the literature for a number of traits in various aquatic species are given in Table – 1.

In *Penaeus stylirostris*, a crustacean to which group *Artemia* also belong, Lester (1988) reported heritability values of 1.31 ± 0.61 and 1.09 ± 0.81 for post larva 1 and mysis 1 respectively, from full sib analysis. All the heritability values estimated in the present work from full sib data are on the higher side and, therefore, must be viewed with caution. The heritability estimates from the regression of offspring on parents must be considered as the realistic and should be used for prediction of correlated response in *Artemia*. The estimates from b_{op} reveals that while traits like length on 3rd day and 6th day as well as number of offsprings in the first lay low to moderately heritable in the narrow sense, traits like age and length at sexual dimorphism and at the time of first offspring laid were poorly heritable, indicating a corresponding level of additive genetic variance for the traits.

Correlation between selected and unselected traits

Association between the two traits, which can be directly observed, is called phenotypic correlation. This may be due to either genetic or environmental factor, or combination of both. The magnitude and direction of correlated response to selection, among other factors, depend upon the genetic correlation between selected and unselected traits. Genetic correlation estimates permit prediction of correlated response in the unselected traits, due to selection for primary trait. Environmental correlation is the correlation of environmental deviations together with non-additive genetic deviations. In the present study genetic, phenotypic and environmental correlations of the selected trait i.e. naupliar length with other traits like length on 3-days of age, length on 6 days of age, length at sexual dimorphism (in both the sexes) and with age at first offspring laid, length at first offspring laid and number of offsprings laid (in females) were estimated. The correlations were initially estimated within sex / generation / line basis and then pooled over generations for each line within sex.

Though the individual estimates of genetic and phenotypic correlations of naupliar length with length on 3 days of age and 6 days of age varied between generations, the pooled estimates were positive in males as well as females of both the lines excepting for the length on 6 days of age in BNS females. The environmental correlations were predominantly negative for length on 3 days of age, but fluctuated between positive and negative direction in case of the length on 6 days of age. The correlated responses realized in both these traits (Tables 39 & 40) actually corroborate the validity of the direction of the pooled

estimates *viz.* a decrease in length on 3 and 6 days of age in SNS line and an increase in BNS line, excepting 6 day length of BNS females.

Although the pooled estimates of genetic and phenotypic correlations of naupliar length with length at sexual dimorphism were of low magnitude, they were invariably positive in direction. Environmental correlation fluctuated between moderate to low values with positive or negative direction. An increase in the length at sexual dimorphism was observed as the correlated response in both the lines, although it was expected only in BNS line.

Genetic and phenotypic correlations of naupliar length with age at sexual dimorphism, pooled over generations were negative in both sexes of SNS and BNS males, but positive in BNS females. Environmental correlations were also negative in most of the generations. The effect of these genetic correlations were not properly reflected in the correlated responses of age at sexual dimorphism.

Although the pooled estimates of genetic and phenotypic correlations of naupliar length with age and length at first offspring laid fluctuated greatly in magnitude, they were always positive in direction, in both the lines. Environmental correlations fluctuated from positive to negative directions with moderate to high values. Correlated response showed an increase in both the SNS and BNS lines.

The pooled estimates of genetic correlation of naupliar length with number of offsprings laid by the females in the first brood were negative and of medium magnitude in both the lines. Phenotypic correlations were of very low magnitudes, being positive in SNS line but negative in BNS line. Environmental correlations fluctuated between positive and negative with low to high values.

The dissimilarity among the sexes and lines with regards to the direction and magnitude of the correlations might not be real. It is quite possible that since there is only very low level of correlation, the fluctuation resulting from any sampling error could have negated it and taken the estimate to the opposite direction.

In view of the low levels of genetic correlations between naupliar size and most of the unselected traits observed in this study, only marginal changes are to be expected in these traits in the form of correlated response.

There are only a very few reports on the genetic and phenotypic correlations in aquatic animals *viz.* tilapia (Robinson and Doyle, 1990), rainbow trout (Gunnes and Gjedrem, 1981; Refstie, 1980) and coho salmon (Hershberger *et al.*,1990). There are, however, no reports on the genetic and phenotypic correlation in the *Artemia* to do any sort of comparison with the result of the present study.

RESPONSE TO SELECTION

DIRECT RESPONSE

Selection differential and selection intensities

The ratios of expected selection differential to effective selection differential were very close to 1.0 in almost all the generations of both the lines (Table 31). This means that the expected selection differentials were effective in all the generations. Since almost all the selected individuals have contributed to

the next generation, the inbreeding coefficients were negligible in all the generation of both the lines (Table 6).

The ratio of the effective to the expected selection differential provides a measure of the influence of natural selection. When this ratio is appreciably greater than one, natural selection may be considered to have favoured artificial selection. On the other hand, when this ratio is appreciably smaller than one, it indicates that natural selection has acted against artificial selection. As can be seen from the Table 31, there was fairly good agreement between expected and effective selection differentials in both lines, suggesting that effect of natural selection is probably not that important during artificial selection for naupliar length.

In the present work, selection intensities were of moderate magnitude while the intensities were -0.8011 to –0.3179 and -1.1942 to –0.3797 in males and females of SNS, the corresponding values in BNS line were 0.2461 to 0.7435 and 0.2164 to 0.7687. Lasley (1978) has given the percentage of male and female progenies required for brood stock replacement as 4-5 % and 40-50 % respectively in beef cattle; 1-2 % and 10-15 % respectively in swine and chickens. Such broodstock selection programmes for domestic animals resulted in selection intensities of 2.0 to 2.7 for males and 0.6 to 0.8 for females (Falconer, 1981). In comparison, selection intensities obtained during present study were of lower magnitude. In spite of this, substantial progress could be made in both lines, and the inbreeding coefficient could be kept at minimum (Table 6). Hence, there is ample scope for intensifying the selection intensities and attain higher selection response.

Phenotypic responses

Selection studies in aquatic invertebrates so far have been limited to the bivalve molluscs like cultivable oysters (Newkirk and Halley, 1982,1983), mussels (Mallet *et al.*, 1986) and pearl oysters (Wada, 1996 and Velayudhan, 1996), there being none from the crustaceans including the *Artemia*. On the contrary, lot of work is being carried out on the selective breeding of domesticated land animals such as poultry, cattle, pig and fishes like trout, salmon, tilapia, channel catfish etc. As such, one of the objectives of the present work was to study the response to selection for reduced and increased naupliar lengths which has got a direct bearing on aquaculture, as already explained in the "Introduction". Incidentally, this is the first study of its kind in *Artemia*.

In the present work, bi-directional selection was practised in *A. franciscana*, one for reducing naupliar length (SNS line) and the other for increasing naupliar length (BNS line). Generation-wise phenotypic responses in naupliar lengths realized from selection (Table 33) show that there was a positive phenotypic response in both the lines. The total cumulative decrease in naupliar length from six generations of selection for smaller naupliar size was –45.3177 μm and –37.5220 μm in males and females respectively. These work out to be –9.3057 % and – 7.6486 % of the naupliar size of the base population. Similarly, total cumulative increase in naupliar length from five generations of selection for larger naupliar size were 8.5923 μm and 38.7966 μm in males and females respectively, which indicated an increase by 1.7644 % and 7.9084 % of the naupliar size of the base population. The mean decrease in the naupliar

length per generation in SNS line were -5.7554 μm and -4.9743 μm for males and females respectively. The corresponding increase per generation in BNS line were 0.3833 μm and 5.5222 μm respectively. It can be thus seen that while both the sexes readly responded to selection for decrease in naupliar size in SNS line, there was a differential response to selection for the higher size in BNS line. In BNS line, the females showed 14.5 times higher response than males, while in the SNS line both sexes showed comparable response. It is rather difficult to explain whether this low response in males is due to attainment of the genetically pre-set maximum size for that sex or due to any other reasons.

The point to be noted in this context is that the male nauplii were always smaller than females in both SNS and BNS lines as well as in the base population. The smaller size of males as compared to females may be the nature's provision to enable them to clasp the female quite easily and to maintain buoyancy during copulation. The males might have reached the size limit set by nature and hence the poor response, when selected for larger size.

Very few bi-directional selection studies, with reference to growth, have been reported in aquatic animals. While Moav and Wahlforth (1976) observed no response from five generation of selection for high growth rate in common carp, there was a strong response to selection for slow growth rate. In channel cat fish, Bondari (1983) reported response to selection for body weight and length in both upward and downward directions. Huang and Liao (1990) reported little response to mass selection for high body weight as well as for low body weight in tilapia. Behrends *et al.* (1987) and Rochetta (1996) could not observe any

response to selection for growth in the U.S. tilapia and guppy, respectively. Lack of response was attributed to the prolonged domestication process in these fishes.

Realized genetic gain

Since phenotype is the product of the combined effect of genotype and environment, the realized phenotypic response does not indicate the true genetic gain from selection. Therefore, genetic gain realized in each generation was calculated by subtracting mean control values of each generation from the corresponding selected generation mean (Table 35). Genetic gain, calculated after subtraction of mean control values from selected generation mean, is free of environmental effects, and therefore, gives the true genetic gain realized from selection.

The cumulative genetic gain in SNS line after six generations of selection for decrease in naupliar size were –41.7244 μm and –38.7585 μm in males and females respectively. Corresponding values of genetic gains after five generations of selection in BNS line for increase in naupliar size were 12.6427 μm in males and 39.4836 μm in females. The realized genetic gain per generation estimated as the regression of cumulative genetic gain on generation number, were –5.2585 μm and –5.2289 μm in males and females of SNS line and 0.9338 μm and 5.3493 μm in BNS line.

It can be seen from the comparison of genetic gains with phenotypic gains that, though the environment had played a role in deviating the phenotypic response from genetic response, its effect was comparatively low. Most of the documented selection studies in the aquatic species have reported the response to

selection without considering the environmental effects. Therefore, they indeed represent phenotypic response only, and not the genetic response.

It can be seen from this study that, selection of males for smaller naupliar size (in SNS line) resulted in a better genetic response than the selection for bigger naupliar size (in BNS line). Different rates of response to bi-directional selection for the same trait have been reported in common carp by Moav and Wohlforth (1976). Though, they did not get any response from five generations of within spawn selection for high growth rate, a relatively strong response was realized from three generations of selection for slow growth. It was suggested that selection for high growth had reached a plateau, involving overdominance, which maintains genetic variation. In the present study, selection in both directions responded positively, though the rate of response was relatively of lower magnitude in the line selected for bigger naupliar size.

Predicted genetic gain

The predicted genetic gain was estimated by formula $R = i\sigma p h^2$ in which 'h^2' is pooled heritability of trait under selection, 'σ_p' is average phenotypic deviation and 'i' is average selection intensity. Selection intensities and phenotypic standard deviations used for prediction were of almost similar magnitudes in males and females of both the lines. Separate predictions were made using both the heritabilities, *viz.*, the estimate from full sib analysis as well as parent offspring regression. Predictions with the full sib heritabilities, were of very high magnitude. Comparison of the predicted and realized genetic gains were used to evaluate the efficiency of selection. In the present study, as can be

seen from Table 36, while prediction based on b_{op} was more or less in agreement with realized genetic gain, the prediction using heritability estimates of full sib were much higher than the realized gains. Gjerde (1986) has concluded that predicted responses to selection usually prove to be overestimates, probably because most sources of bias cause an overestimation of heritability values. Similar observations are made in the present study also. Thus, while the prediction of response using heritability from full sib data are far from the realized response, the prediction based on the b_{op} heritabilities are more or less comparable to the realized response. This fact suggests that the heritability estimated from the full sib data were indeed inflated by non-additive genetic variances, environmental co-variances, maternal effects etc., unlike the heritability from b_{op} which contains only additive genetic variance. Therefore, it will be advisable to use only heritability estimates from parent-offspring regression for prediction of selection response in naupliar size.

The ratios of realized gains to predicted gains b_{op} were high in both the sexes of SNS and females of BNS, indicating high efficiency of selection in the present study. Comparison of these ratios revealed that the values were highest in SNS male selected for smaller naupliar size, but very low in BNS males selected for high naupliar size. It is a well known fact that when ratio exceeds unity, as observed in SNS males of the present study, it indicates that natural selection is also favouring the artificial selection. When the ratio is close to zero, it indicates natural selection acting against artificial selection. As a corollary, it can be presumed that nature prefers smaller males and bigger females. As discussed

elsewhere, while bigger males beyond the optimum size, may not be preferable for the buoyancy during copulation, bigger females may be ideal for reproductive and maternal requirements.

However, there are no reports on the predicted and realized genetic gains in *Artemia*, to compare with the findings of this study.

Clayton *et* al. (1957) stated that both predicted and realized responses to selection would be in close agreement, only at higher intensities of selection. The realized response at lower intensities is usually below expectation. The genetic gain realized in the present study really commensurate with the predicted gains (based on b_{op}) even though the selection intensities were of moderate magnitude. Hence, there is ample scope to improve the response by enhancing the selection intensity.

Time trend in phenotypic standard deviation

In the present study, phenotypic standard deviations of naupliar size estimated generation-wise were of moderate magnitude in males and females of both the lines. This enabled us to keep the selection intensities at moderate magnitude and to avoid inbreeding. While the phenotypic standard deviation showed reducing trend in males with the advancement of selection, it was not so in the females. However, these changes were of very low magnitude and statistically non-significant. As the *A. franciscana* base population was raised from the wild stock without any previous selection or even domestication, a substantial amount of variability is naturally expected in the stock even after six generations of selection. It implies that since the phenotypic standard deviations has changed only slightly in magnitude even after a number of generations of

selection, there exists scope for further improvement through continued selection. The very low and non-significant values of regression heritability estimates of naupliar size on generation numbers, observed in this study also support this view. Due to the lack of selection studies in crustaceans, reports of the time trend in phenotypic variability associated with selection are also not available for further comparisons.

Realized heritability

Pirchner (1983) proposed that when epistasis, dominance and common environmental effects are unimportant, heritability estimates from the regression of offspring on parents should also correspond to realized heritability. In the present study, while the realized heritabilities of females of both the lines were almost close to the heritabilities from parent-offspring regression, there were considerable variations in males. As stated above, such variation can be caused by factors like epistasis, dominance and common environment, which substantially affect the naupliar size. Reports of considerable variations between the realized and estimated heritabilities are available in the literature. For example, while the realized heritability in *Oreochromis niloticus* was –0.05 for increase in body weight (Teichert-Coddington, 1983), the heritability estimates based on sire offspring regression ranged from 0.04 to 0.10 for body growth (Tave and Smitherman, 1980). There are no reports, however, on realized heritability in *Artemia*.

CORRELATED RESPONSE

Realized response in unselected traits

The realized response in the correlated traits such as length on 3rd day of age, length on 6th day of age, length at sexual dimorphism, age at sexual dimorphism, age at first offspring laid, length at first offspring laid and number of offsprings in first brood, as a result of selection for naupliar length, have been presented in Tables 39 to 45. Selection for reduced naupliar length in SNS line brought about a simultaneous reduction in 3rd day length, 6th day length and the number of offsprings in first brood, and an increase in traits like age at sexual dimorphism, length at sexual dimorphism, age at first offspring laid and length at first offspring laid. Selection for bigger naupliar length (BNS line) brought about simultaneous increase in length on 3rd day and 6th day of age in males, length at sexual dimorphism, in both sexes and age at first offspring laid, length at first offspring laid and age at sexual dimorphism in females. However, traits like number of offsprigs in first brood, length on 3rd day and 6th day of age in female and age at sexual dimorphism in males, registered a decrease in BNS line. Although the selected generation mean differed significantly from the base generation means, the average response per generation were not statistically significant, except that of the number of offspring laid in the first brood.

The phenotypic parameters with respect to life history and reproductive characteristics *viz.* total life span, time between the broods, percentage of offspring encysted, broods per female, offspring per day per female, total offspring per female, pre-reproductive period, reproductive period and post-reproductive period were measured from the selected lines, on completion of the

selection. Comparison of these values with those of the base generation were made to assess the correlated changes in them (Table 46). This comparison indicated that age at the time of first offspring laid and time between broods increased in both the lines. While the total life span registered an increase in SNS, it remained almost same in BNS. Though the total number of offsprings produced per female registered an increase in SNS line, but reverse was the case in BNS. Similarly, while the total number of broods decreased in both the lines, the total numbers of offsprings produced increased in SNS line. Pre-reproductive, reproductive and post-reproductive periods showed only slight variations.

Expected response in unselected traits

Expected responses in the correlated traits estimated from the full sib heritabilities (Table 47) were of higher magnitude than those from parent offspring heritabilities (Table 48) as in the case of selected trait. As described earlier, the very high values of expected response estimated from full sib heritability may be due to the fact that these heritability values have been inflated by non-additive genetic variance, environmental co-variance, maternal effect etc., unlike the b_{op} heritabilities which contains only the additive genetic variance. In the SNS line, the expected responses for length at 3 days and 6 days of age were negative like those of realized correlated response in them, but the expected and realized gains were not in agreement for length at sexual dimorphism. Expected responses for age at sexual dimorphism in both sexes and number of offsprings laid in females of SNS were positive. While the realized response in age at sexual dimorphism showed a trend similar to the expected response, reverse trend was observed for number of offsprings laid in first brood.

Expected response in age and length at first offspring laid were negative, whereas the realized gains were in the opposite direction.

In the BNS line, expected responses and correlated realized responses showed similar trends in direction, except the length on 3 days of age, in females.

According to Bell (1972), expected genetic gain in the correlated trait is based on genetic relations of additive pleotropic genes affecting the selected and unselected traits. Futher, since the correlation due to non-additive genes and interaction among the genes are beyond estimation, certain amount of discrepancy between observed and expected correlated responses is inevitable. Bohren *et al.* (1966) and Kinney & Shoffner (1967), in their studies on terrestrial animals, stated that the prediction of correlated responses was likely to be less accurate than prediction of direct response itself. As such, the disparity between predicted and realized responses observed in some of the correlated traits is understandable.

None of the work on aquatic animals, particularly dealing with invertebrates have cited the estimation of expected responses and their relationship with the realized responses.

In brief it can be said that valuable information on the quantitative genetics of *A. franciscana* could be elicited from this pioneering study, which had remained unexplored hitherto. For example, the heritability values of naupliar size and other quantitative traits using the two standard methods, besides the genetic, phenotypic and environmental correlations have been estimated for first time in *Artemia*. Similarly, the present study has indicated the presence of a fairly high amount of additive genetic variance which could be exploited through

individual selection. The effectiveness of using the selective breeding techniques for developing *Artemia* with altered naupliar sizes has also been demonstrated in this work.

Although the changes observed after selection in SNS and BNS lines may not be outstandingly decisive, they have nevertheless proved the usefulness of selective breeding programme for developing two divergent lines, smaller naupliar size (SNS) for penaeid larvae and bigger naupliar size (BNS) for fish larvae, ornamental fishes etc. It is thus, a noteworthy contribution in paving way for large scale selective breeding programme for developing different lines to suit the requirement of various species of cultured animals.


SUMMARY

SUMMARY

Artemia nauplii have a unique position in aquaculture industry especially for larval nutrition. Since the size of nauplius is one of the important criteria for effective forage, there exists a need for evolving lines/strains of different size specifications to suit the requirements of various species of cultured animals, through selective breeding techniques. This calls for an in-depth genetic knowledge of *Artemia* especially with reference to its quantitative genetics. However, there is hardly any reported work in this area and the present investigation was, therefore, initiated with following objectives:

1. To characterize *Artemia franciscana* with respect to its quantitative traits of importance.
2. To estimate the variability in the above traits and to partition them into different constituent components.
3. To estimate and compare heritabilities of various quantitative traits using different methods.
4. To carry out selective breeding of *Artemia* for naupliar size (length) and to estimate the genetic gain realized from selection.
5. To estimate correlated response in the unselected traits.
6. To evaluate efficiency of selection from the comparison of predicted and realized responses.

Artemia franciscana was chosen for the study in view of its small naupliar size, sexual breeding behaviour and its major share in the commercial use. The nauplii were obtained from the foundation stock cyst belonging to batch NO. 425 G, 06345 of Supreme, San Francisco Bay Brand of INVE Aquaculture, Inc. The trait under selection was naupliar size. Bi-directional mass selection was practised to develop divergent stocks. The base population was divided into three equal parts to be designated as Small Naupliar Size (SNS) line, Big Naupliar Size (BNS) line, and Control line. The criterion of selection was smaller naupliar size in SNS line and larger naupliar size in BNS line, while there was no selection in control line.

The unselected traits evaluated in detailed for the genetic parameters and for correlated response were:

a) Length on 3 days of age.

b) Length on 6 days of age

c) Length at sexual dimorphism

d) Age at sexual dimorphism

e) Length at first offspring laid

f) Age at first offspring laid

g) Number of offsprings in the first brood

The highlights of the results are presented below:

1. Phenotypic parameters: The mean length of nauplii in the base generation was 486.9912 ± 2.1136 μm for males and 490.5754 ± 1.8157 μm for females. Mean lengths recorded for 3 days of age, 6 days of age and at sexual dimorphism were 1.8679 mm , 4.1005 mm and 3.8004 mm respectively in male,

and 1.8712 mm, 4.2990 mm and 3.9053 mm respectively in females. The length of females at the time of first offspring laid was 10.0888 mm. Mean age at sexual dimorphism was 5.8861 mm days in males and 7.9761 days in females. The mean values for age at first offspring laid and total number of offsprings laid in the first brood were 16.00 days and 53.6696 respectively.

The mean naupliar lengths of females were consistently more than those of males, both in base as well as selected generations, although the differences were not always significant statistically. The size differences between sexes, however, persisted and increased with advancing age.

2. Heritability of naupliar length: The heritability estimates of naupliar length, from the regression of progeny on parents, pooled over generations, were 0.2123 $\pm$ 0.0766 and 0.3885 $\pm$ 0.1108 for males and females respectively in SNS line. The corresponding estimates in BNS were 0.5777 $\pm$0.1154 and 0.3364 $\pm$0.1176 respectively. The heritability estimates from full sib data, pooled over generations, were 1.3256 $\pm$ 0.0474 and 1.1004 $\pm$ 0.0522 for males and females respectively in SNS line, whereas the corresponding estimates in BNS were 1.2580 $\pm$ 0.0583 and 1.4221 $\pm$ 0.0479 respectively. While the moderate values of heritability estimated from b_{op} indicated existence of fairly good amount of additive genetic variance which can be exploited through simple selective breeding techniques, the very high estimates of heritability from full sib analysis indicated existence of non-additive genetic variances also.

3. Heritability of correlated traits: The heritability estimates for length on 3 days of age, length on 6 days of age, length at sexual dimorphism and age at

sexual dimorphism in males and females of both lines, and length at first offspring laid, age at first offspring laid and number of offsprings in first brood in the females of both the lines were estimated from parent offspring regression as well as full sib analysis and were pooled over generations. The pooled heritability estimates from regression of offspring on parent were medium to moderate in magnitude, whereas those from full sib data were moderate to very high.

4. Realized heritability: Realized heritability values were moderately high except for a few negative values. The mean realized heritabilities in males and females were 0.4550 and 0.3056 in SNS line and -0.0085 but 0.3143 in BNS line.

5. Genetic, phenotypic and environmental correlation: Sex-wise and generation-wise estimates of the genetic, phenotypic and environmental correlations between naupliar length and other traits were estimated from both the lines, and these estimates were then pooled over the generations. Genetic correlations were generally positive for all the traits except the age at sexual dimorphism and number of offspring in first brood.

6. Selection differentials: Expected and effective selection differentials were of almost the same magnitude in both the lines except the second generation of BNS line. These selection differentials, averaged over generations, were slightly higher in females of both SNS and BNS lines. Their mean values were -16.6780 μm and -16.3966 μm in SNS males, -19.9266 μm but -22.3101 μm in SNS females, 16.2308 μm and 15.8700 μm in BNS males and 17.1180 μm and 17.0019 μm in BNS females.

The ratios of expected selection differentials to effective selection differential were generally close to unity in most of the generations of both the lines, indicating that expected selection differentials were effective in all the generations, and that natural selection did not influence artificial selection. Since almost all selected individuals had contributed to next generation, the inbreeding coefficient was negligible in all generations of both the lines.

7. Phenotypic responses: The phenotypic response in naupliar length from selection was quite substantial. The naupliar size in SNS line, from six generations of selection for smaller naupliar size, could be reduced from 486.99 μm and 490.58 μm to 441.67 μm and 453.05 μm in males and females respectively. The cumulative gain for males and females were -44.32 μm and – 37.52 μm respectively with average gain per generation being –5.76 μm and – 4.97 μm.

In the BNS line, the naulpiar size could be increased to 495.58 μm and 529.37 μm in males and females from 486.99 μm and 490.58 μm in the base generation, through five generations of selection for bigger naupliar size. The total gain worked out in males and females were 8.59 μm and 38.80 μm with mean gain of 0.39 μm and 5.52 μm respectively. The mean phenotypic responses were statistically significant except for BNS males.

8. Realized genetic gain: Most of the phenotypic responses realized from selection were due to genetic gains. In the SNS line, total genetic gain realized from six generations of individual selection for reduction of the naupliar length was -41.7244 μm in males and -38.7585 μm in females. Whereas in BNS line,

the total genetic gain from five generations of selection were 12.6427 μm and 39.4836 μm in males and females respectively.

The realized mean genetic gain per generation, estimated from regression of control corrected generation means on generation numbers was -5.2585 μm in males and -5.2289 μm females of SNS and 0.9338 μm in males and 5.3493 μm in females of BNS line. The mean genetic gains were fairly high and statistically significant except in BNS males.

9. Expected genetic gains: Expected responses were calculated using the heritability estimated from regression of offspring on parent (b_{op}) and also full sib heritability. While, estimates as per former were close to realized genetic gains, those from latter were on the higher side. This result indicates that heritability estimates from full sibs are indeed inflated by non-additive genetic variance, unlike the b_{op} which includes only additive genetic variance.

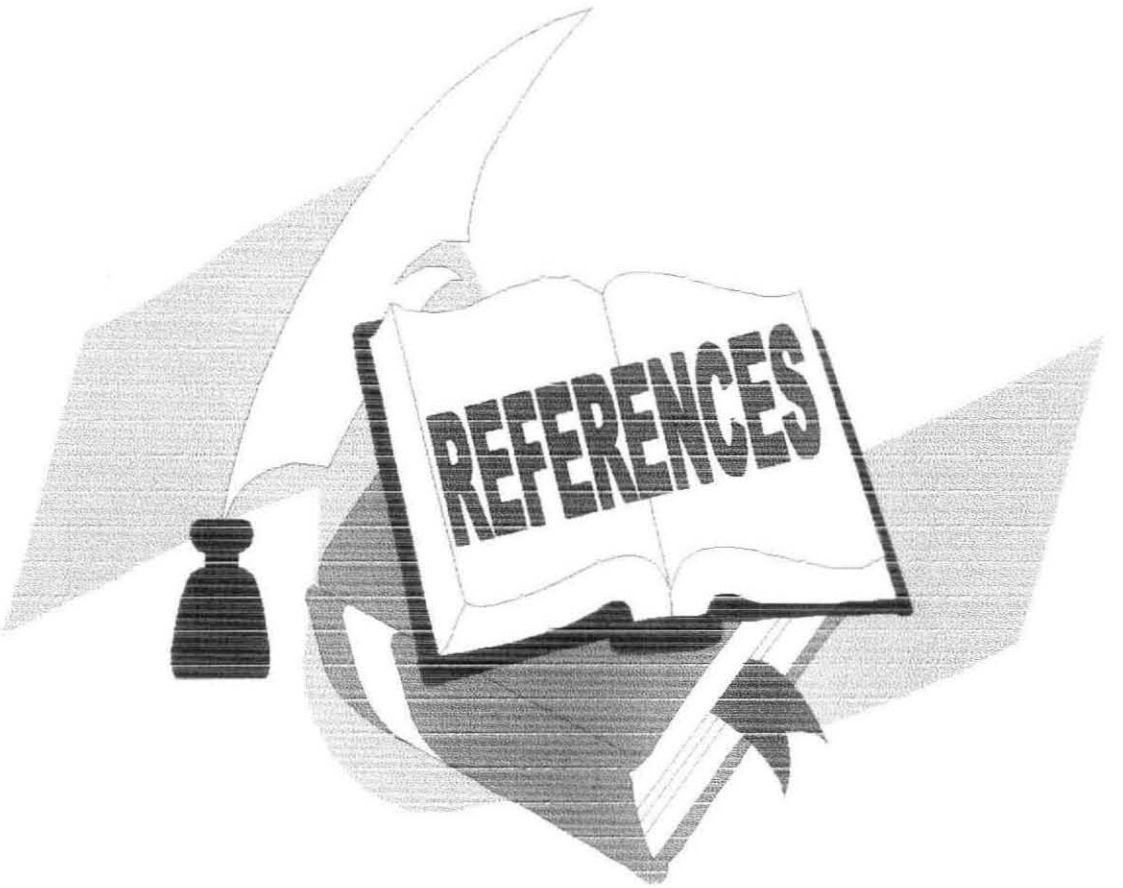
10. Trends in phenotypic standard deviation: The regression of phenotypic standard deviation on generation number, though showed a declining trend in males and an increasing trend in females, as the generations of selection advanced, they were of very low magnitude and statistically non-significant indicating the presence of unexhausted variability in the stock even after the selection. The regression coefficients were -0.5315 μm ± 0.7441 and -1.0421 μm ± 0.6030 in males of SNS and BNS lines respectively, while the corresponding values in females were 1.2871 μm ± 1.0667 and 1.4256 μm ± 0.4039.

11. Correlated response: Selection for smaller naupliar length brought about a simultaneous reduction in length on 3rd day and 6th day length and the number

of offsprings in first brood, but an increase in age at sexual dimorphism, length at sexual dimorphism, age at first offspring laid and length at first offspring laid. Selection for bigger naupliar length in BNS line brought about simultaneous increase in length on 3rd day and 6th day length in males, length at sexual dimorphism in both the sexes and age at sexual dimorphism, age at first offspring laid and length at first offspring laid in females. However, there was a decrease in the number of offspring in the first brood and length on 3rd day and 6th day of age in females and age at sexual dimorphism in males.

Comparison of base generation with the fifth and sixth selected generation of BNS and SNS line with respect to remaining lifehistory and reproductive traits indicated the following correlated changes:

Age at first offspring laid was observed to have increased in both the selected lines as compared to the base. While the total life span registered an increase in SNS line, it remained almost same in BNS line. Time between the broods increased in both the lines *vis-a-vis* the base generation. Total number of offspring produced per female increased in SNS but decreased in BNS as compared to base population. Though the total number of offsprings produced increased in SNS line the total number of broods decreased in both the lines. Pre-reproductive, reproductive and post-reproductive periods also showed slight variation as compared to the base population.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